2000

Ecology of Seagrass Fishes and Macroinvertebrates on Guatemala's Atlantic Coast.

Alejandro Arrivillaga
Louisiana State University and Agricultural & Mechanical College

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

Bell & Howell Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

UMI®

ECOLOGY OF SEAGRASS FISHES AND MACROINVERTEBRATES ON GUATEMALA'S ATLANTIC COAST

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Oceanography and Coastal Sciences

by
Alejandro Arrivillaga
B.S., Universidad del Valle de Guatemala, 1984
M.S., Instituto Politecnico Nacional, Mexico, 1988
May, 2000

DEDICATION

I want to dedicate this dissertation to my wife, Catalina Lopez, who unselfishly sacrificed her own academic career so that I could pursue my Doctorate.

ACKNOWLEDGMENTS

I wish to express my most sincere appreciation to my Major Professor, Dr. Donald M. Baltz, for his guidance and friendship throughout my doctoral studies. I would also like to thank the members of my committee, Drs. James Geaghan, William Kelso, Irving Mendelssohn, and Joseph Siebenaller for their valuable suggestions and review of this manuscript.

Several sources provided support to finance my studies in the U.S., including the Fulbright-Latin American Scholarships Program of American Universities (LASPAU), the Organization of American States Regular Training Program, the Universidad de San Carlos de Guatemala's Programa de Apoyo a Maestrias y Doctorados en el Exterior, and a graduate assistantship from the Coastal Fisheries Institute, Louisiana State University. Sources of funds for the field research were provided by a grant from the Paseo Pantera Program of Wildlife Conservation Society.

In Guatemala, I had the help of the Quinto Family of Puerto Barrios, Izabal and from Jorge Luis Galindo during all phases of field work. In Guatemala City my parents, Juan and Grace Arrivillaga-Cortez provided their hospitality and support. I would also like to thank Drs. Eric Swensen, and John Day, Coastal Ecology Institute, and Karen McKee, Wetland Biogeochemistry Institute, Louisiana State University, for providing access to their laboratory equipment for sediment and plant analyses. Drs. Kenyon Lindeman, University of Miami, Darryl Felder, University of Louisiana at Lafayette, and Sarah LeCroi, Gulf Coast Research Laboratory, Mississippi, provided assistance with grunts, xanthid-goneplacid crabs and hermit crabs identification, respectively. Dr. Jacoby

Carter, National Wetlands Research Center, USGS, provided much needed support and empathy during the final months of my dissertation writing and defense.

Lastly, I would like to recognize my wife, Caty, and my children, Javier and Adrian for their love, encouragement, and support throughout these long years of graduate school in the U.S., away from home, and in a new environment.

TABLE OF CONTENTS

ABSTRACT

The ecology of fishes and macroinvertebrates inhabiting shallow seagrass beds was studied at Bahia La Graciosa, located in Amatique Bay in the Caribbean coast of Guatemala. The study area included extensive turtle grass, *Thalassia testudinum*, meadows over muddy substrate, whereas a more exposed shoreline also supported turtle grass meadows over sandy substrates outside the bay. A total of 166 samples were collected across two seasons and habitat types in three sampling trips to the area with a cylindrical drop sampler. Diversity and abundance of fishes and macroinvertebrates inhabiting seagrass and adjacent bare-sand sites were described to assess the relative importance of seagrasses as nurseries. Utilization of seagrass meadows by fishes and decapod crustaceans was also described for exposed (beach) and protected (bay) habitat types. Seagrass fish and decapod crustacean community structure was compared between beach and bay habitat types during rainy and dry season months. Total crustacean and fish densities, species diversity, and evenness were several times higher in seagrass beds compared to bare-sand substrates, with no significant differences in gastropod densities between habitats. The majority of the fishes collected on seagrass were juveniles, supporting the hypothesis that seagrass is an important nursery habitat. When comparing beach and bay habitat sites, total fish and decapod crustacean densities were similar, but densities of individual species differed significantly between habitat types. Over half of the species were present in both seasons and almost half of the species were present in both habitat types; however, significant interactions were detected between season and habitat for densities of the most abundant species. Significant differences in fish and decapod

crustacean community structures were detected with analyses of similarities between habitat types, but the same analyses between seasons were significant only for fishes. An analysis of complex ecological gradients revealed that the highest variability was related, in decreasing order, to seagrass abundance, habitat type, and seasonal variables.

CHAPTER 1

INTRODUCTION

Seagrasses are highly productive flowering plants that often form vast meadows over shallow unconsolidated sediments in coastal areas. Their influence on coastal processes and their importance to mankind may be summarized as follows: seagrasses significantly modify the physical, chemical, and sedimentological properties of coastal areas, they provide nutrients, energy, and nursery habitats that sustain coastal fishery resources, and they provide foraging grounds for both fisheries and endangered marine species (Heck and Orth, 1980; Ogden, 1980; Orth, 1992). The most common seagrasses in tropical and temperate regions are turtle grass, *Thalassia testudinum*, and eel grasses, *Zostera* spp. (Zieman and Zieman, 1989).

Seagrasses ecosystems possess high rates of primary productivity and growth, comparable and often exceeding that of terrestrial agricultural crops. Moreover, because of their high standing crop and the fact that few organisms feed directly on them, seagrasses produce large amounts of dissolved and particulate detritus, which play major roles in coastal trophic dynamics. They also stabilize their habitat by slowing water currents, promoting sedimentation, and reducing resuspension of both inorganic and organic materials. The structurally complex water column provided by their dense leaf baffle forms shelter for an extremely diverse fauna of all trophic levels (Phillips 1992).

Seagrass fish assemblages are composed largely of immature individuals; therefore seagrasses have often been identified as nurseries for many marine species, including commercially important fishes (Weinstein and Brooks, 1983; Blaber et al., 1992). The

presence of abundant food for small fishes is another important feature of seagrass beds (Pollard, 1984; Robertson, 1984). Previous studies have shown high macroinvertebrate diversity in seagrasses resulting from complex biotic and abiotic interactions (Orth, 1992). The epifauna living on turtle grass in the Caribbean region includes particulate feeders, grazers, and carnivores that feed on different members of the turtle grass community (Kikuchi and Perez, 1977; Ogden 1980). In addition, zooplankton densities in seagrass beds may be twice as high as in offshore environments (Robertson et al., 1988). In spite of all the benefits derived from seagrasses, these coastal communities are threatened by environmental stressors and have experienced decreases in faunal abundance and reductions in plant biomass (Lubbers et al., 1990; Heck and Crowder, 1991).

The effect of hydrodynamic regimes on seagrass structure has been observed (Fonseca and Bell, 1998), as has as the role of seagrasses in altering water column velocity and wave energy (Fonseca et al., 1983; Fonseca and Cahalan, 1992). Seagrasses can significantly reduce wave energy and enhance sediment stability (Fonseca and Cahalan, 1992) by baffling currents and damping wave action (Orth, 1977). Seagrass coverage decreases wave height and physical stress at the sediment-water interface, with suspended sediment concentrations being lower within seagrass beds compared to unvegetated sand. Many studies, mostly in temperate areas, have explored the effect of exposure to tidal currents and wave energy on seagrass faunal abundance and composition (Orth, 1977). Factors such as degree of exposure, seagrass coverage, and sediment structure primarily affect the composition and quantity of mobile epibenthic fauna (Phil,1986). Low-energy continuous seagrass beds have significantly higher shrimp density than high-energy patchy

beds (Murphey and Fonseca, 1995); however, significantly higher numbers of macrobenthic epifaunal and infaunal species in exposed turtle grass beds compared with protected have also been reported (O'Gower and Wacasey, 1967).

Seasonal factors, including food availability, larval supply, and differential temporal availability of adjacent habitat types, are known to affect seagrass nekton distribution (Orth and van Montfrans, 1987; Pollard, 1984; Rozas and Minello, 1998). In temperate seagrass systems, for example, fluctuations in invertebrate abundance and species richness appear to be consequences of predation and seasonality. Seasonal changes in seagrass structural complexity brought about by variation in water temperature can strongly influence nekton (Heck, 1979). In the tropics, lower species abundances seem to coincide with periods of reduced salinity associated with rainfall, but fluctuations are smaller than those in temperate systems because predators are present year round and because the magnitude of seasonal environmental variation is less than in temperate systems (Heck, 1979; Winstein and Heck, 1979).

Common management problems in seagrass ecosystems are often connected to terrestrial modifications due to human activities (e.g., coastal resort development, urban and agricultural practices, and upland deforestation). In several Latin American countries, coastal development of resorts with boat marinas have caused loss of seagrass resources (Phillips 1992). Other impacts include fishing practices that uproot seagrass shoots, uncontrolled urban waste and debris release into near-shore coastal waters, release of industrial, mineral, and biological wastes, exploration and exploitation for oil, and port construction, including wharfs, dikes, and channel dredging that raises silt plumes into the

water (Onuf 1994). Considering these threats, the most pressing research need for Latin America's seagrasses is to conduct surveys of coastal areas to determine distribution, abundance, and status of the various seagrass species and the fauna associated with them.

Bahia La Graciosa is a shallow coastal lagoon located in the east side of Amatique Bay in the Gulf of Honduras on the Atlantic coast of Guatemala. An artificial channel, Canal Inglés, connects Bahia La Graciosa through Rio San Francisco to the Caribbean on the eastern shore of the Punta de Manabique. Bahia La Graciosa is surrounded by red mangrove forests and includes extensive seagrass meadows, consisting mainly of turtle grass. The area provides support for local rural and urban Guatemalans through both fishery and recreational uses of its natural resources. Sandy substrates dominate the mouth of the bay, whereas most of the interior bay is dominated by clay-silt substrates. The mean depth inside the bay is 2 m and at the mouth is 1.5 m. Tidal range in the area is small, with a maximum of 1 m. The climate is tropical and seasonal variation is limited. The primary freshwater influence in the region is from Rio Dulce, located on the western side of the Amatique Bay; however, direct precipitation into the Bahia La Graciosa drainage is also important. Rainfall occurs throughout the year with a maximum monthly mean of 43.4 cm in August and a minimum monthly mean of 14.2 cm in March. A vaguely defined dry season occurs between January and May and the rainy season occurs between June and December.

The Atlantic coast of Guatemala, though not very long (200 km of coastline), supports important commercial and artisanal fisheries. Previous studies (Bortone et al., 1988) have suggested Bahia La Graciosa as a possible nursery for both fishes and

macroinvertebrates, due in large part to the presence of its extensive seagrass beds and surrounding mangrove forests. This system is believed to support much of Guatemala's fishery production on the Atlantic coast. Although the area is relatively undisturbed, tourism development that does not fully consider seagrass conservation is planned for the area.

The objectives of this study were to: 1) quantify the nursery value of healthy turtle grass beds in the Atlantic coast of Guatemala in a relatively pristine area, before further baseline degeneration, 2) analyze influences of environmental factors, particularly exposure to wave action, on seagrass fish and decapod crustacean communities, and 3) evaluate the effects of dry and rainy seasons and protected and exposed habitat types on the community structure of fishes and decapod crustaceans. A community was defined, according to Crowder (1990), as a group of populations that occur in a common area and that interact with one another. Differences in community structure were described in terms of species composition and by comparing the rank order abundances of the species (Grossman et al., 1982; Herbold, 1984). In Chapter 2, biological diversity, community structure, and species abundance in adjacent sandy, shallow-water seagrass and bare-sand sites are compared. In Chapter 3, community structure of fish and decapod crustaceans and the density of common species in protected and exposed seagrass habitat types are examined, as are diel differences in species composition and abundance. In Chapter 4, constancy of differences and similarities in fish and decapod crustacean community structures between exposed and protected habitat types across seasons are examined. Chapter 5 provides an summary of the results and conclusions.

References

Blaber, S. J. M., D.T. Brewer, J.P. Salini, J.D. Kerr, and C. Conacher. 1992. Species composition and biomasses of fishes in tropical seagrasses at Groote Eylandt, Northern Australia. Est. Coast. Shelf Sci. 35: 605-620.

Bortone, S.A., R.L. Shipp, W.P. Davis, and R.D. Nester. 1988. Artificial reef development along the Atlantic coast of Guatemala. Northeast Gulf Sci. 10: 45-48.

Crowder, L.B. 1990. Community ecology. Ch. 19: 609-632 *in* C.B. Schreck and P.B. Moyle, eds. Methods for Fish Biology. American Fisheries Society, Bethesda Maryland.

Fonseca, M.S., J.C. Zieman, G.W. Thayer, and J.S. Fisher. 1983. The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. Estuar. Coast. Shelf Sci. 17, 367-380.

Fonseca, M.S. and J.A. Cahalan. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. Estuar. Coast. Shelf Sci. 35, 565-576.

Fonseca, M.S. and S.S. Bell. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. Mar. Ecol. Prog. Ser. 171, 109-121.

Grossman, G.D., P.B. Moyle, and J.O. Whitaker Jr. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. Amer. Nat. 120, 423-454.

Heck, K.L. Jr. 1979. Some determinants of the composition and abundance of motile macroinvertebrate species in tropical and temperate turtlegrass (*Thalassia testudinum*) meadows. J. Biogeogr. 6: 183-200.

Heck, K.L. Jr. and R.J. Orth. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. Pages 449-464 *in* V. S. Kennedy, ed. Estuarine perspectives, Academic Press, New York.

Heck, K.L. Jr. and L.B. Crowder. 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. Ch. 14: 281-295 *in* S. S. Bell, E. D. McCoy and H. R. Mushinsky, eds. Habitat Structure: The physical arrangements of objects in space. Chapman and Hall, New York. 434 pp.

Herbold, B., 1984. Structure of an Indiana stream fish association: choosing an appropriate model. Amer. Nat. 124, 561-572.

Kikuchi, T. and J.M. Perez. 1977. Consumer ecology of seagrass beds. Pages 147-194 *in* C. P. McRoy and C. Helfferich, eds. Seagrass Ecosystems: A Scientific Perspective. Marcel Edkker Inc. New York.

Lubbers, L., W.R. Boynton, and W.M. Kemp. 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. Mar. Ecol. Prog. Ser. 65: 1-14.

Murphey, P.L. and M.S. Fonseca. 1995. Role of high and low energy seagrass beds as nursery areas for *Penaeus duorarum* in North Carolina. Mar. Ecol. Prog. Ser. 121, 91-98.

O'Gower, A.K. and J.W. Wacasey. 1967. Animal communities associated with *Thalassia*, *Diplanthera*, and sand beds in Biscayne Bay. I. Analysis of communities in relation to water movement. Bull. Mar. Sci. 17, 175-210.

Ogden, J.C. 1980. Faunal relationships in Caribbean seagrass beds. Pages 173-198 *in* R. C. Phillips and C.P. McRoy, eds. Handbook of seagrass biology: an ecosystem perspective. Garland STPM Press, New York.

Onuf, C.P. 1994 Seagrasses, dredging and light in Laguna Madre, Texas, USA. Estuar. Coast. Shelf Sci., 39: 75-91.

Orth, R.J., 1977. The importance of sediment stability in seagrass communities. In: B.C. Coull (ed.) Ecology of Marine Benthos. University of South Carolina Press, Columbia, pp. 281-300.

Orth, R.J., and J. van Montfrans. 1987. Utilization of a seagrass meadow and tidal marsh creek by blue crabs Callinectes sapidus. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. Mar. Ecol. Prog. Ser. 41: 283-294.

Orth, R. J. 1992. A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. Pages 147-164 *in* D. M. John, S. J. Hawkins, and J. H. Price, eds. Plant-Animal Interactions in Marine Benthos. The Systematics Association Special Volume No. 46. Clarendon Press, Oxford.

Pihl, L. 1986. Exposure, vegetation and sediment as primary factors for mobile epibenthic faunal community structure and production in shallow marine soft bottom areas. Neth. J. Sea Res. 20, 75-83.

Phillips, R.C. 1992. The seagrass ecosystem and resources in Latin America. In: Ulrich Seeliger (Ed.): Coastal Plant Communities of Latin America, Ch. 7. Academic Press, Inc. San Diego. 107-121.

Pollard, D.A. 1984. A review of ecological studies on seagrass-fish communities, with particular reference to recent studies in Australia. Aquat. Bot. 18: 3-42.

Robertson, A.I. 1984. Trophic interactions between the fish fauna and macro benthos of an eelgrass community in Western Port, Victoria. Aquat. Bot. 18: 135-153.

Robertson, A.I., P. Dixon, and P.A. Daniel. 1988. Zooplankton dynamics in mangrove and other nearshore habitats in tropical Australia. Mar. Ecol. Prog. Ser. 43: 139-150.

Rozas, L.P. and T.J. Minello. 1998. Nekton use of salt marsh, seagrass, and nonvegetated habitats in a South Texas (USA) estuary. Bull. Mar. Sci. 63: 481-501.

Weinstein, M.P. and Brooks, H.A. 1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: community composition and structure. Mar. Ecol. Prog. Ser. 12: 15-27.

Weinstein, M.P. and K.L. Jr. Heck. 1979. Ichthyofauna of seagrass meadows along the Caribbean coast of Panama and in the Gulf of Mexico: composition, structure and community ecology. Mar. Biol. 50: 97-107.

Zieman, J.C. and R.T. Zieman. 1989. The ecology of the seagrass meadows of the west coast of Florida: a community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85: 155 pp.

CHAPTER 2

COMPARISON OF FISHES AND MACROINVERTEBRATES ON SEAGRASS AND BARE-SAND SITES ON GUATEMALA'S ATLANTIC COAST[1]

Introduction

Seagrasses are extremely productive, diverse, and valuable marine resources. They include more than 50 species of vascular plants inhabiting shallow waters in diverse coastal environments. The most common seagrasses in tropical and temperate regions are turtle grass, *Thalassia testudinum*, and eel grasses, *Zostera* spp., respectively (Zieman and Zieman, 1989). Manatee grass, *Syringodium filiforme*, and shoal grass, *Halodule wrightii*, are also found in the Caribbean (Ogden, 1980). Seagrass meadows support highly diverse fish and macroinvertebrate communities around the world (Ogden, 1980; Heck and Orth, 1980; Orth, 1992), and are essential nursery areas for juvenile fishes, shrimp, and crabs (Ogden and Gladfelter, 1983; Weinstein and Brooks, 1983; Pollard 1984; Zieman and Zieman, 1989; Blabber et al., 1992; Connolly, 1994a; Perkins-Visser et al., 1996). Furthermore, seagrasses support adult fishes foraging on the rich and varied faunas associated with these structurally complex habitat types, and their importance to marine and estuarine species of commercial and recreational value has been widely demonstrated (Ogden, 1980; Ogden and Gladfelter, 1983; Middleton et al., 1984; Heck and Crowder, 1991; Bell et al. 1992; Connolly, 1994a).

---

[1]First published as: Arrivillaga, A. and D.M. Baltz. 1999. Comparison of fishes and macroinvertebrates on seagrass and bare-sand sites on Guatemala's Atlantic coast. Bull. Mar. Sci. 65: 301-319. This text incorporates editorial changes suggested by my Graduate Committee. See Appendix for copyright permission.

Distinguishing characteristics of seagrass communities, including elevated primary and secondary productivity, abundance of organisms, and species diversity, are particularly apparent when compared to adjacent unvegetated sites (Heck and Orth, 1980; Ogden, 1980; Orth, 1992; De Trooch et al., 1996). The high primary productivity of seagrasses and associated epiphytes is channeled to consumers primarily through the detritus food chain (Zieman et al., 1984), and a considerable amount of seagrass organic material is also exported to other systems (Ogden, 1980; Orth, 1992; Pergent et al., 1997). Contrasts between seagrasses and bare sites are not restricted to differences in the number of species and individuals, but also to differences in the relative abundance of species (Bell and Pollard, 1989).

Seagrass fish assemblages are composed largely of immature individuals, therefore seagrasses have often been identified as nurseries for many marine species, including commercially important fishes (Weinstein and Brooks, 1983; Blaber et al., 1992). The direct value of seagrasses as fish nurseries is primarily based on the refugia that seagrasses provide from predation pressure, resulting in reduced mortality, although feeding links also have been found (Pollard, 1984; Lubbers et al., 1990; Pergent et al., 1997). Some fishes make ontogenetic movements to other habitat types upon reaching a critical size at which seagrasses no longer provide adequate shelter (Robertson and Duke, 1987). Other hypotheses suggest that habitat complexity, hydrodynamic effects on larval supply, and stable substrates may also contribute to the increased abundance and species diversity of seagrass fish communities (Rozas and Odum, 1988). The main nursery function of seagrass beds is associated with shelter resource; however, the refugia component and the

benefits seagrass food resources provide to fishes and macroinvertebrates are difficult to separate.

The presence of abundant food for small fishes, especially the macrobenthic fauna, is another important feature of seagrass beds (Pollard, 1984; Robertson, 1984). Previous studies have shown high macroinvertebrate diversity in seagrasses resulting from complex biotic and abiotic interactions (Orth, 1992). The epifauna living on turtle grass in the Caribbean region includes particulate feeders, grazers, and carnivores which feed on the different members of the *Thalassia* community (Kikuchi and Perez, 1977; Ogden 1980). In addition, zooplankton densities in seagrass beds have been found to be twice as abundant as in offshore environments (Robertson et al., 1988). In spite of all the benefits derived from seagrasses, these coastal habitat types are threatened by environmental stressors and they have experienced decreases in faunal abundance and reductions in plant biomass (Lubbers et al., 1990; Heck and Crowder, 1991; Sheridan, 1992).

The primary objective of this study was to quantify the nursery value of healthy seagrasses for fishes and macroinvertebrates on the Atlantic coast of Guatemala in a relatively pristine area, before further baseline degeneration (Pauly, 1995). We characterized the biological diversity, community structure, and species abundances in adjacent sandy, shallow-water seagrass and bare-sand sites to test the null hypothesis of no faunal differences between habitat types. We also characterized the environmental conditions in terms of physical, chemical, and biotic variables between habitat types. Finally, we characterized meiofaunal assemblages in seagrass and adjacent bare-sand sites to compare abundances and community structure as a probable indicator of food

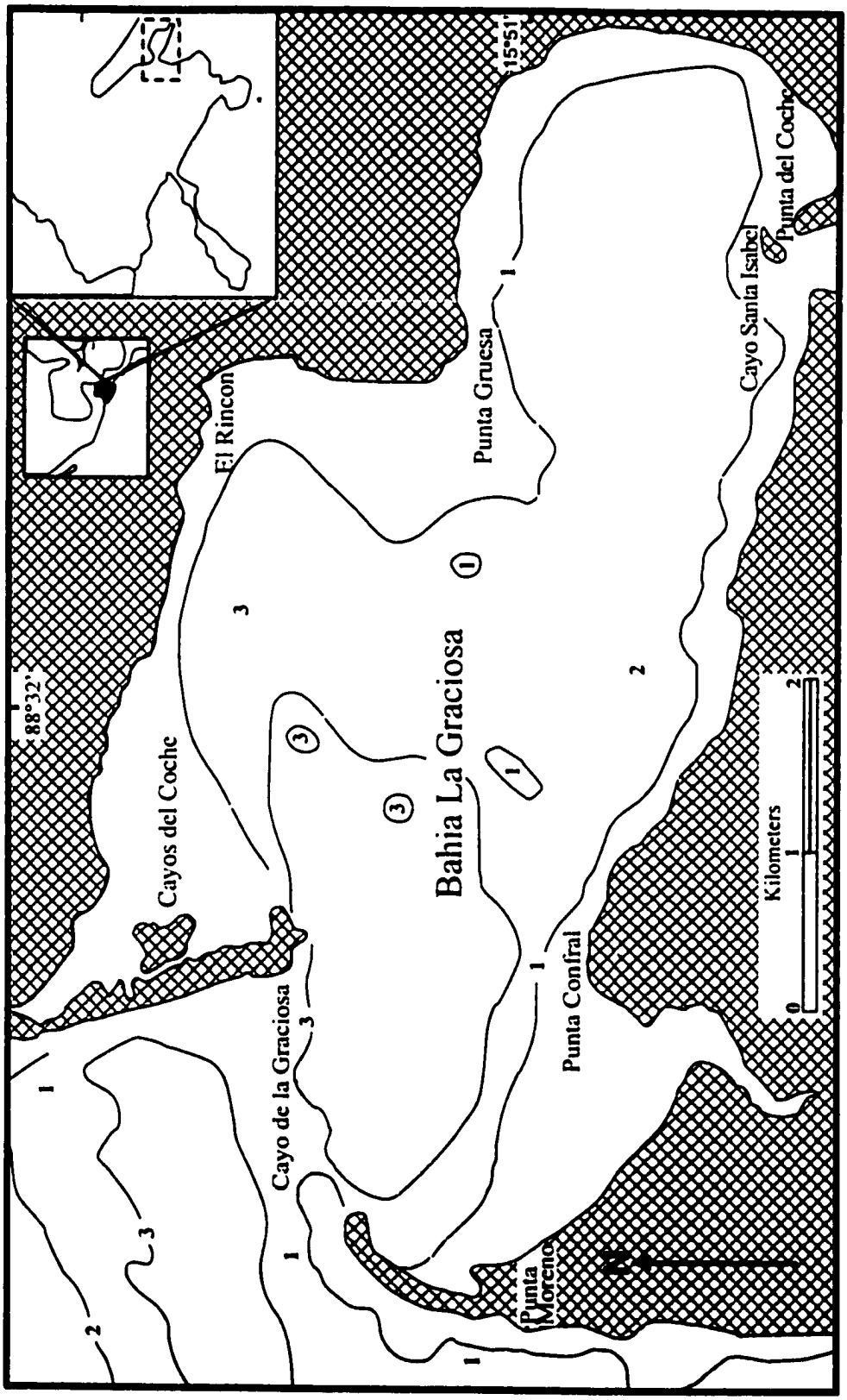
availability for fishes and macroinvertebrates. This was the first quantitative study of seagrass fishes and macroinvertebrates conducted to assess the fishery value of seagrasses on Guatemala's Atlantic coast, an area of local economic and ecological importance currently under development.

Materials and Methods

Study Area

The study area was located at the mouth of Bahia La Graciosa, on the Caribbean coast of Guatemala (Fig. 2.1). Bahia La Graciosa, located on the eastern shore of Amatique Bay, is a shallow coastal lagoon, surrounded by red mangrove (*Rhyzophora mangle*) forests, whereas includes an extensive seagrass community, consisting mainly of turtle grass. Sandy substrates dominate the mouth of the bay, while most of the interior bay is dominated by clay-silt substrates. The mean depth inside the bay is 2 m and at the mouth is 1.5 m. The shallow, high wave energy conditions typical of the study area differ substantially from nearby seagrass meadows occurring in adjacent deeper or lower energy environments (Arrivillaga, unpublished data). Tidal range in the area is small with a maximum of 1 m. The primary freshwater influence in the region is from Rio Dulce, located on the western side of the Amatique Bay, but direct precipitation into the Bahia La Graciosa drainage is also important. Rainfall occurs throughout the year (mean annual precipitation is 3.1 m) with a monthly maximum of 389 mm in October and a minimum of 120 mm in March. An artificial channel, Canal Inglés, connects Bahia La Graciosa through Rio San Francisco to the Caribbean on the eastern shore of the Punta de Manabique. The Atlantic coast of Guatemala, though not very long (200 km of coastline),

Figure 2.1. Map of the study area, Bahia La Graciosa, Guatemala (depths in fathoms).



supports important commercial and artisanal fisheries. Previous studies (Bortone et al., 1988) have suggested Bahia La Graciosa as a possible nursery for both fishes and macroinvertebrates, believed to support much of Guatemala's fishery production on the Atlantic coast.

Sample Collection and Analysis

Equal areas of vegetated and unvegetated substrates were sampled during daylight hours between 14-17 December 1993 with a cylindrical drop sampler (1.18 m^2) consisting of a metal skirt and clear acrylic walls to reduce faunal visual avoidance. This sampling method allowed for quantitative, instantaneous evaluation of organisms present within a determined area (Gilmore, 1990) and provided information on microhabitat utilization (Zimmerman et al., 1984; Baltz, 1990; Baltz et al., 1993). The sampler was suspended from a boom extending 2 m beyond the bow of a small (6 m) boat and about 0.4 m above the water. A pull-pin release mechanism was used to drop the sampler on randomly selected sites within sampling strata. Upon deployment, and after firmly setting the sampler, a seawater solution of powdered rotenone (5%) was applied, and the fishes and macroinvertebrates swimming to the surface were collected with dip nets. We then swept the entire basal area thoroughly with landing nets (Cummings Model 270-12", 5 mm mesh) to capture any remaining organisms. We continued sweeping until three successive passes yielded no organisms. Small specimens were preserved directly in 95% ethanol. Larger organisms were preserved with 10% buffered formalin solution and then transferred to 95% ethanol. Individuals were identified to species (Böhlke and Chaplin, 1968; Fisher, 1978; Allen, 1987; Anderson, 1987), counted, and measured to the nearest

millimeter in standard length (SL for fishes), carapace width (CW for crabs), or carapace length (CL for shrimp).

We conducted a stratified random sampling survey of bare-sand and seagrass strata over the range of depths covered by the sampler (0 - 1 m). Sampling was designed to avoid differences in environmental variables, other than plant coverage, and to collect an equal number of samples between seagrass-dominated and adjacent bare-sand sites. Thirteen samples were collected on each strata. Five additional samples were collected on intermediate seagrass densities (1- 25% cover) and were used for a correlation analysis between percent cover and faunal abundance. We recorded microhabitat data at each sampling site, including minimum and maximum depths, distance to the shore, substrate type (sand or mud), bottom visibility, turbidity in NTU (Monitek, model 21 PE portable nephelometer), mid-water column velocity (Montedoro-Whitney model PVM-2A portable velocity meter), water temperature (pocket thermometer), salinity (temperature-compensated refractometer, AO model 10419), dissolved oxygen concentration (YSI dissolved oxygen meter Model 57), percent of the bottom covered by seagrass, and shore vegetation.

Seagrass biomass and leaf data were obtained by collecting a 10 cm^2 core sample of the grasses to a substrate depth of 10 cm with every drop sample. Seagrass leaf biomass (g dry wt·m^{-2}) was estimated by drying seagrass leaves (above-ground, green blades) in an oven at 60°C to constant weight (Ott, 1990). We included any attached epiphytes and carbonate materials, but roots, rhizomes (short and long shoots), and drift algae were excluded (Sheridan, 1992). We also estimated leaf surface area index (m^2 leaf

area · m^{-2} substrate) from measurements of leaf length and width (above-ground, green blades) (Bulthuis, 1990).

Meiofaunal samples were obtained with every drop sample with a random sediment core collected at each site (2 of the seagrass core samples were accidentally destroyed). We used a modified plastic syringe (2.6 cm inner diameter, 5.30 cm^2 area) to sample to a substrate depth of 2.6 cm. Samples were preserved in the field in 10% formalin in sea water. In the laboratory, the meiofauna (organisms passing through a 0.5 mm sieve and retained on a 0.063 mm sieve) was stained with Rose Bengal and extracted from the sediment following the Ludox extraction protocol of Fleeger and Chandler (1983). Organisms where then identified to major taxonomic categories and counted. Meiofauna abundances were $\log_e (x+1)$ transformed prior to statistical testing for differences between seagrass and bare-sand sites. Number of meiofauna taxa, meiofauna taxa diversity, and individual meiofauna abundances for the most frequent taxa (present in >40% of samples) were also tested. The remainder of the sediment sample was analyzed for percent sand content by separating the sand and fines fractions and obtaining their respective dry weights.

For both environmental and faunal data sets, residuals were analyzed for normality with the Normality Procedure of SAS (Schlotzhauer and Littell, 1987). Because of a lack of normality in fish, crustacean, and gastropod abundance data, $\log_e (x+1)$ transformations were used to normalize distributions prior to comparing abundances between seagrass and bare-sand samples. Hotelling's T^2 Test (Littell et al., 1991) was used to compare means of total number· m^{-2}, species diversity (Shannon's H'), Margalef's species richness (D)

(Margalef, 1968), and evenness (J) (Pielou, 1975) for fishes, crustaceans, and gastropods. Hotelling's T^2 is a multivariate test of H_0: $\mu=\mu_0$ where μ and μ_0 are vectors of response variable means from two populations, and its likelihood ratio is equivalent to the Wilk's *lambda* of a MANOVA with two populations (Johnson and Wichern, 1992). If the observed value of T^2 is large, then H_0: $\mu = \mu_0$ is unlikely to be true and is, therefore, rejected (Johnson and Wichern, 1992). The same test was used for the environmental and meiofaunal data sets. When overall significant differences between bare-sand and seagrass sites where found with Hotelling's T^2 test, a Tukey's posterior test ($\alpha = 0.05$, with the BonFerroni correction) was performed to determine which of the variables were significantly different

We examined cumulative diversity plots to determine if we had adequately characterized the faunal groups with our sampling procedure, to estimate the community diversity (H'_{pop}, *sensu* Pielou, 1966), and to compare community diversity between strata. First, samples selected in random order were pooled in sequence and their diversities calculated at each sample addition for each strata. This process was repeated 10 times and the mean cumulative diversity was calculated for each sample addition step (Livingston et al., 1976). Next, a negative exponential function similar to Von Bertalanffy's equation (Ricker, 1975) was fitted to the cumulative-diversity-step means with a non-linear regression procedure (SAS Institute Inc. 1985). The line produced by the model:

$$H'_C = H'_A*(1-\exp(-k*(x-x_0))),$$

where H'_C = cumulative diversity, H'_A = asymptotic cumulative diversity, k = exponential change rate, x = number of cumulative samples, and x_0 = theoretical number of cumulative

samples corresponding to $H'_C = 0$, was plotted together with the cumulative diversity step means and visually examined to determine whether or not they approached asymptotic. Finally, the point at which cumulative-diversity-step means approached an asymptote (t in Pielou, 1966) was identified as the number of cumulative samples that resulted in less than a 10% increase in cumulative diversity (Mueller-Dombois and Ellenberg, 1974). Using this value, we estimated community diversity (H'_{pop}) and its sampling variance (Pielou, 1966). Community diversity comparisons between strata for a faunal group were considered significantly different if the 95% confidence intervals (CI) for H'_{pop} did not overlap.

To assess the effect of intermediate values of seagrass density on faunal abundance, scatter plots and Pearson's correlation coefficients of seagrass coverage versus fauna abundance and diversity were examined. Data from the 26 drop samples previously described, together with the five extra samples from areas with intermediate (1 - 60% cover) seagrass percent cover values, were used for the plots and correlation analyses. All plant abundance variables were highly correlated. Correlation of leaf biomass and leaf area index was particularly high ($r = 0.9726$; $p<0.0001$). Correlation between percent cover and leaf biomass and leaf area index were 0.6567 ($p<0.0001$) and 0.5997 ($p<0.0003$), respectively; therefore, seagrass percent cover was selected to represent seagrass density.

Results

In the primary analytical design (Table 2.1), a total of 26 drop samples were collected between seagrass and bare-sand strata. We were unable to detect significant

Table 2.1. Environmental data for the December 1993 samples (mean ± 1 SE) collected near the mouth of Bahia La Graciosa, Guatemala, in seagrass covered and bare-sand bottom types. Differences in means of physico-chemical variables between strata were non-significant (Hotelling's $T^2 = 17.51$, df = 25, $P > 0.233$), and seagrass variables were not tested.

Variable	Seagrass	Bare-sand	Combined
Mean depth (cm)	67.31 ± 5.67	57.31 ± 4.95	62.31 ± 3.82
Temperature (°C)	23.78 ± 0.20	23.88 ± 0.18	23.83 ± 0.13
Salinity (ppt)	16.38 ± 0.42	17.23 ± 0.43	16.81 ± 0.30
Dissolved oxygen (ppm)	7.6 ± 0.19	7.51 ± 0.17	7.55 ± 0.13
Water velocity ($cm \cdot s^{-1}$)	0.02 ± 0.00	0.01 ± 0.00	0.02 ± 0.00
Turbidity (NTU)	1.42 ± 0.43	0.81 ± 0.11	1.12 ± 0.23
Sediment % sand content	98.06 ± 0.59	98.26 ± 0.31	98.16 ± 0.33
Distance to shore (m)	96 ± 25	79 ± 25	87 ± 17
Seagrass:			
Percent cover	79.62 ± 3.69	0 ± 0	-
Biomass ($g\ dw \cdot m^{-2}$)	44.22 ± 9.64	0 ± 0	-
Leaf surface area index ($m^2 \cdot m^{-2}$)	1.06 ± 0.26	0 ± 0	-
Sample size	13	13	26

differences (Hotelling's $T^2 = 16.04$, df = 25, $P > 0.11$) for temperature, salinity, dissolved oxygen, mean depth, water velocity, sediment percent sand content, and turbidity between strata. Variation in distance to the shore was substantial (4 to 300 m range) but not significant between strata. In vegetated sites, percent seagrass cover ranged from 60 to 100%, seagrass blade biomass ranged from 7.0 to 132.3 g dry wt·m^{-2}, and leaf surface area index ranged from 0.4 to 3.5 m^2 leaf area · m^{-2} of substrate (Table 2.1).

Faunal collections included 276 fishes and macroinvertebrates from 35 species (i.e., 16 fishes, 14 crustaceans, and 5 gastropods). Of those, 222 specimens (34 species) where present on seagrass dominated sites, compared to only 54 specimens (six species) on bare-sand sites. Fish and macroinvertebrate community structure differed substantially between adjacent habitat types: 16 fish, 14 crustacean, and four gastropod species were collected on seagrass sites while only 1, 3, and 2 species, respectively, were found on bare-sand sites (Table 2.2). Fishes and crustaceans were 20 and seven times more abundant, respectively, in seagrass compared to adjacent bare-sand sites (Table 2.2). Seventy fishes collected on seagrass sites (Table 2.2) represented the Lutjanidae, Gerreidae, Syngnathidae, Gobiidae, and Labridae, with two species each, and the Haemulidae, Dactiloscopidae, Scaridae, Clinidae, Batrachoididae, and Labrisomidae with one species each (Robins et al., 1990). The most abundant species was the juvenile Latin grunt, *Haemulon steindachneri* (K. Lindeman, pers. comm.), although it was present in only one sample. Second in abundance was the shortchin stargazer, *Dactyloscopus poeyi*, the only fish collected on bare-sand sites. The emerald parrotfish, *Nicholsina usta*, was third in abundance and was also the most frequently occurring species (30%) in seagrass

Table 2.2. Mean (± 1 SE) fish, crustacean, and gastropod abundance, number of individuals · m^{-2} collected near the mouth of Bahia La Graciosa, Guatemala, in December 1993, in seagrass and bare-sand covered bottoms.

Species	Seagrass	Bare-sand	Combined
Fishes:			
Haemulon steindachneri	2.28 ± 2.28	0 ± 0	1.14 ± 1.14
Dactyloscopus poeyi	0.33 ± 0.23	0.20 ± 0.14	0.26 ± 0.13
Nicholsina usta	0.33 ± 0.15	0 ± 0	0.16 ± 0.08
Malacoctenus aurolineatus	0.26 ± 0.15	0 ± 0	0.13 ± 0.08
Halichoeres pictus	0.26 ± 0.26	0 ± 0	0.13 ± 0.13
Eucinostomus argenteus	0.20 ± 0.20	0 ± 0	0.10 ± 0.10
Eucinostomus gula	0.13 ± 0.09	0 ± 0	0.07 ± 0.05
Paraclinus fasciatus	0.13 ± 0.09	0 ± 0	0.07 ± 0.05
Cosmocampus elucens	0.13 ± 0.09	0 ± 0	0.07 ± 0.05
Lophogobius cyprinoides	0.13 ± 0.13	0 ± 0	0.07 ± 0.07
Lutjanus grisceus	0.07 ± 0.07	0 ± 0	0.03 ± 0.03
Lutjanus purpureus	0.07 ± 0.07	0 ± 0	0.03 ± 0.03
Batrachoides gilberti	0.07 ± 0.07	0 ± 0	0.03 ± 0.03
Bathygobius soporator	0.07 ± 0.07	0 ± 0	0.03 ± 0.03
Halichoeres vivittatus	0.07 ± 0.07	0 ± 0	0.03 ± 0.03
Cosmocampus brachycephalus	0.07 ± 0.07	0 ± 0	0.03 ± 0.03
Number of species	16	1	16
Crustaceans:			
Pagurus (c.f.) *critinicornis*	1.37 ± 0.38	0.39 ± 0.23	0.88 ± 0.24
Periclimenes longicaudatus	0.98 ± 0.45	0 ± 0	0.49 ± 0.24
Palemonetes vulgaris	0.72 ± 0.42	0 ± 0	0.36 ± 0.22
Callinectes danae	0.46 ± 0.28	0.26 ± 0.15	0.36 ± 0.16
Farfantepenaeus notialis	0.33 ± 0.20	0.07 ± 0.07	0.20 ± 0.11
Alpheus armillatus	0.26 ± 0.20	0 ± 0	0.13 ± 0.10
Panopeus bermudensis	0.20 ± 0.10	0 ± 0	0.10 ± 0.05
Clibanarius vittatus	0.13 ± 0.09	0 ± 0	0.07 ± 0.05
Euripanopeus abbreviatus	0.13 ± 0.13	0 ± 0	0.07 ± 0.07
Sicyonia laevigata	0.13 ± 0.13	0 ± 0	0.07 ± 0.07

(table continued)

Hippolyte curacaoensis	0.07 ± 0.07	0 ± 0	0.03 ± 0.03
Microphrys bicornutus	0.07 ± 0.07	0 ± 0	0.03 ± 0.03
Periclimenes americanus	0.07 ± 0.07	0 ± 0	0.03 ± 0.03
Rimapenaeus constrictus	0.07 ± 0.07	0 ± 0	0.03 ± 0.03
Number of species	14	3	14
Gastropods:*			
Nassarius polygonatus	3.11 ± 0.84	1.75 ± 0.35	2.43 ± 0.47
Nerita virginica	2.53 ± 1.02	0 ± 0	1.26 ± 0.56
Jaspidella jaspidea	0 ± 0	0.71 ± 0.38	0.36 ± 0.20
Thais haemastoma	0.06 ± 0.06	0 ± 0	0.03 ± 0.03
Prunum apicinum	0.06 ± 0.06	0 ± 0	0.03 ± 0.03
Number of species	4	2	5

* Additional mollusc (namely bivalves) were collected but not quantitatively sampled.

samples, followed by the goldline blenny, *Malacoctenus aurolineatus*. Fishes collected in our samples were primarily juveniles and ranged in size from 12 to 69 mm SL; but about 80% of the fishes captured were <40 mm SL.

Fourteen species (N=68 individuals) of crustaceans were collected on seagrass sites whereas only nine specimens of three species were collected in bare-sand samples (Table 2.2). Dominant crustaceans in seagrass samples were the hermit crab, *Pagurus* (cf.) *critinicornis*, the longtail grass shrimp, *Periclimenes longicaudatus*, and the marsh grass shrimp, *Palemonetes vulgaris*. Penaeid shrimp were represented by two species, the southern pink shrimp (*Farfantepenaeus notialis*) and the roughneck shrimp (*Rimapenaeus constrictus*). The two penaeid species were present on seagrass sites, but only southern pink shrimp was collected on bare-sand sites. Hermit crabs and Dana swimming crabs (*Callinectes danae*) dominated bare-sand samples and southern pink shrimp ranked third in abundance. All Dana swimming crabs collected were juveniles less than 42 mm CW.

Eighty-four gastropods collected on seagrass sites represented four species (Table 2.2). The dominant species, *Nassarius polygonatus* and *Nerita virginica* (50 and 31% of combined seagrass and bare-sand gastropod abundance, respectively), were present in over 30% of the samples. These two species were also the most abundant (44 and 45% of total, respectively) and frequently occurring gastropods in seagrass samples (61 and 54%, respectively). Two other gastropods, *Thais haematosa* and *Prunum apicium*, were also present in seagrass samples. Bare-sand samples included only 42 specimens of two species, with only one species common to both habitat types. The most abundant gastropods in sand samples were *N. polygonatus*, and *Jaspidella jaspidea* (62 and 26%,

respectively). The frequency of occurrence on bare-sand sites was highest for *N. polygonatus* (77%), followed by *J. jaspidea* (23%).

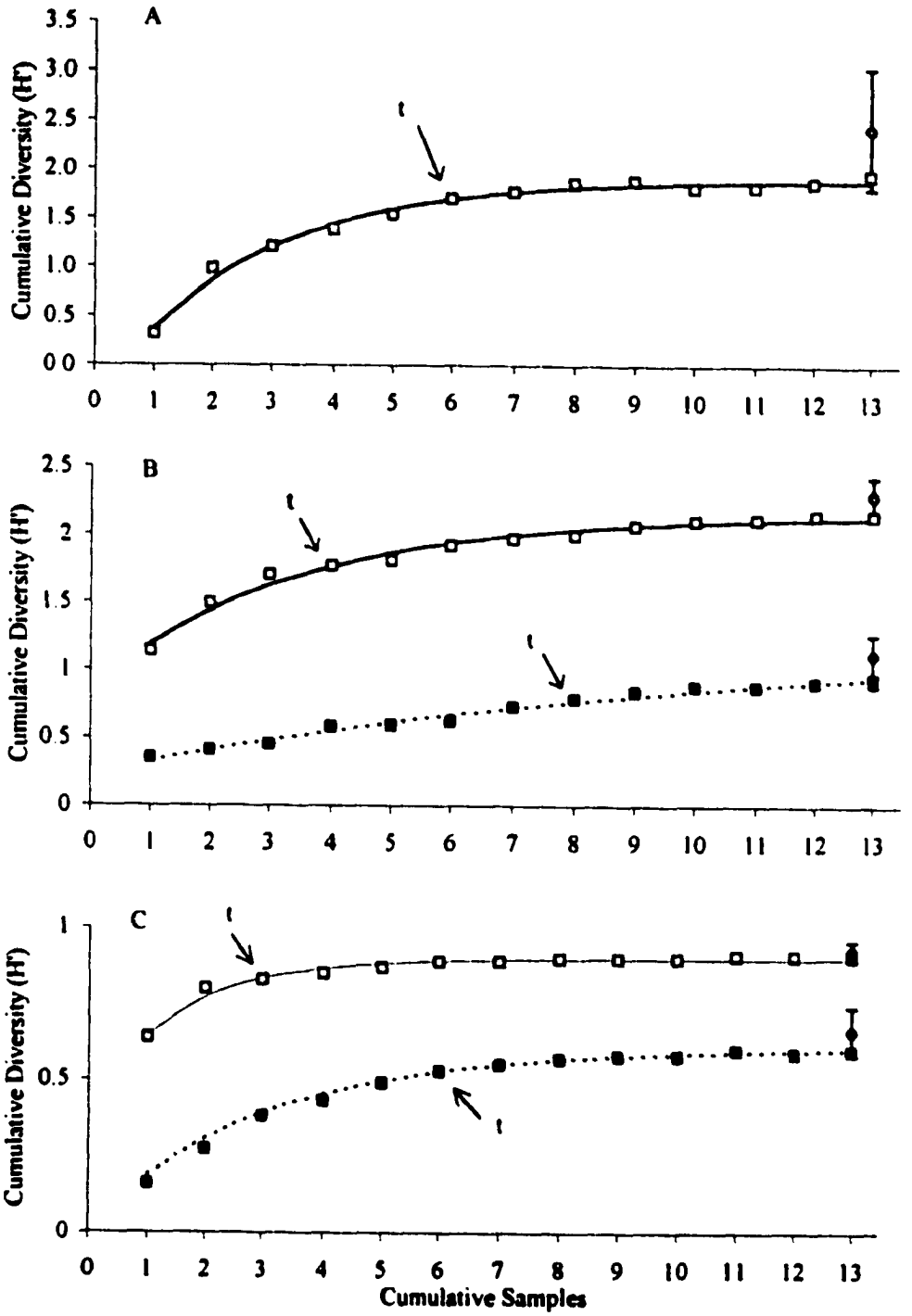
Several measures of faunal abundance and diversity differed significantly between strata (Hotelling's $T^2 = 77.30$, df = 25, $P < 0.0660$) (Table 2.3). Based on a comparison of equal areas, combined abundances of crustaceans and fishes were significantly higher on seagrass sites (Tukey's test, df = 24, $P < 0.01$) than on bare-sand sites (Table 2.3); however, differences in gastropod abundances between strata were not significant (Tukey's test, df = 24, $P > 0.05$). Fish and crustacean species richness (Margalef's D) were both significantly higher in seagrass strata (Tukey's test, df = 24, $P < 0.01$), whereas differences in gastropod species richness was non-significant (Tukey's test, df = 24, $P > 0.32$). Species diversity and evenness were significantly higher in seagrass strata for fishes and crustaceans (Tukey's test, df = 24, $P < 0.01$), but these variables were not different for gastropods (Tukey's test, df = 24, $P > 0.32$).

Plots of cumulative diversity for the major macrofaunal groups approached an asymptote with fewer than 13 samples, indicating adequate characterization of these community descriptors. Less than a 10% increase in cumulative diversity (H'_C) was observed with six samples for fishes collected on seagrass sites (Fig. 2.2A), with four and eight samples for crustaceans on seagrass and bare-sand, respectively (Fig. 2.2B), and with three and six samples for gastropods on seagrass and bare-sand sites, respectively (Fig. 2.2C). Fish community diversity ($H'_{pop} \pm 95\%$ CI) in seagrass strata was estimated at 2.44 ± 0.62. Fish community diversity on bare-sand sites was zero. Crustacean community diversity was 2.30 ± 0.13 on seagrass and only 1.12 ± 0.14 on bare-sand sites,

Table 2.3. Mean (± 1 SE) faunal abundance and diversity for samples collected near the mouth of Bahia La Graciosa, Guatemala, in December 1993, in seagrass covered and bare-sand bottoms. Overall comparisons indicated significant differences (Hotelling's T^2 = 77.30, df = 25, P < 0.0198). In posterior testing, significant (Tukey's test, df = 24, P < 0.01) differences between strata are indicated by *.

Variable	Seagrass	Bare-sand	Combined
Fishes:			
Total number · m^{-2}	4.56 ± 2.15*	0.20 ± 0.14*	2.38 ± 1.14
Diversity (H')	0.49 ± 0.16*	0 ± 0*	0.25 ± 0.09
Margalef's D	0.67 ± 0.22*	0 ± 0*	0.33 ± 0.13
Evenness (J)	0.41 ± 0.13*	0 ± 0*	0.21 ± 0.08
Crustaceans:			
Total number · m^{-2}	4.95 ± 1.34*	0.72 ± 0.25*	2.84 ± 0.79
Diversity (H')	0.79 ± 0.18*	0.05 ± 0.05*	0.42 ± 0.12
Margalef's D	1.04 ± 0.24*	0.11 ± 0.11*	0.57 ± 0.16
Evenness (J)	0.62 ± 0.12*	0.08 ± 0.08*	0.35 ± 0.09
Gastropods:			
Total number · m^{-2}	5.76 ± 1.38	2.46 ± 0.48	4.11 ± 0.79
Diversity (H')	0.33 ± 0.09	0.1 ± 0.07	0.21 ± 0.06
Margalef's D	0.28 ± 0.09	0.09 ± 0.06	0.19 ± 0.06
Evenness (J)	0.44 ± 0.12	0.14 ± 0.09	0.29 ± 0.08
Sample size	13	13	26

Figure 2.2 Sample and community diversity for fishes (A), crustaceans (B), and gastropods (C) for bare sand (■) and seagrass covered (□) bottom samples collected near the mouth of Bahia La Graciosa, Guatemala, in December 1993. Fitted lines represents an exponential increase in cumulative sample diversity on sample size for bare sand (dashed line) and seagrass (solid line) sites, with end points indicating the asymptotic cumulative sample diversity values (H'_{λ}, see text). Letter t indicates the points at which cumulative diversity changed <10%. Community diversity values (H'_{pop}) ± 95% CI are represented for bare-sand (◆) and seagrass (◇) sites (bare-sand fish community diversity was zero).



and non-overlapping 95% CIs indicated significant differences between strata. Gastropod community diversity was 0.93 ± 0.03 on seagrass and 0.66 ± 0.08 on bare-sand sites, and non-overlapping community diversity CIs also indicated significant differences between strata.

When we included an additional five samples from intermediate seagrass densities with the 26 bare-sand and full seagrass cover samples, there were significant positive correlations (df = 30) between seagrass percent cover and fish and crustacean abundance ($r = 0.67$, $p<0.0001$ and $r= 0.51$, $p<0.003$, respectively) and diversity ($r = 0.51$, $p<0.0032$ and $r = 0.64$, $p<0.0001$, respectively). Gastropod abundance was significantly ($r = 0.3855$; $p<0.0322$) correlated with seagrass cover; however, gastropod diversity and species richness did not show significant correlations. Positive correlations of seagrass cover on fish and crustacean faunal abundances were consistent with results obtained from the Hotelling's T^2 test. It was also clear that intermediate seagrass cover values resulted in intermediate values of faunal abundance. The relationship between seagrass abundance and most gastropod variables proved to be non-significant, again coinciding with the multivariate test of significance for seagrass and bare-sand sites, and indicating that low, intermediate, and high plant cover values had similar levels of gastropod species richness and diversity.

In 24 meiofauna core samples analyzed, a total of 12 taxa were found (Table 2.4). Nematodes numerically dominated all samples, constituting about 70.7% of the total meiofauna (overall mean = 274.92 individuals·10 cm^{-2} of sediment). Collectively, oligochaetes, polychaetes, copepodes, and bivalves accounted for over 27% of the total

Table 2.4. Mean (± 1 SE) meiofaunal density, number of individuals·10 cm^{-2} collected near the mouth of Bahia La Graciosa, Guatemala, in December 1993, in seagrass covered and bare-sand bottoms. Significant differences in overall taxa abundances and diversities between strata were not detected (Hotelling's $T^2 = 9.61$, df = 25, $P > 0.08$). Individual taxa comparisons between strata indicated significant differences (Hotelling's $T^2 = 23.75$, df = 25, $P < 0.024$), but in posterior testing only nematodes abundances between strata were significant (Tukey's test, df = 22, $P < 0.01$).

Taxa	Seagrass	Bare-sand	Combined
Overall taxa:			
No. of Individuals	481.13 ± 93.87	310.3 ± 53.54	388.6 ± 53.68
No. of Taxa	6.64 ± 0.51	5.23 ± 0.34	5.88 ± 0.33
Diversity (H')	0.96 ± 0.09	0.80 ± 0.11	0.87 ± 0.08
By Taxa:			
Nematodes	336.54 ± 77.9	222.79 ± 42.84	274.92 ± 43.22
Oligochaetes	48.03 ± 12.31	50.22 ± 13.72	49.21 ± 9.14
Polychaetes	43.22 ± 17.48	15.82 ± 5.87	28.38 ± 8.87
Copepodes	30.53 ± 6.48	10.89 ± 37.90	19.89 ± 4.07
Bivalves	8.92 ± 3.63	2.47 ± 1.01	5.42 ± 1.84
Cnidarians	5.32 ± 5.32	0 ± 0	2.44 ± 2.44
Ostracods	4.29 ± 1.42	5.52 ± 3.83	4.95 ± 2.14
Gastropods	1.54 ± 1.1	0.29 ± 0.20	0.86 ± 0.52
Isopods	1.37 ± 0.57	0.87 ± 0.46	1.1 ± 0.36
Cumaceans	0.69 ± 0.29	0.44 ± 0.23	0.55 ± 0.18
Amphipods	0.51 ± 0.27	0 ± 0	0.24 ± 0.13
Turbelarians	0.17 ± 0.17	1.02 ± 0.70	0.63 ± 0.39
Number of samples	11	13	24

meiofauna and had a frequency of occurrence >40%. Other taxa present in both seagrass and bare-sand strata, in decreasing order of abundance, were ostracods, isopods, gastropods, turbelarians, and cumaceans, with a combined abundance of <1% of the total meiofauna. Differences in meiofauna density, taxa richness, and diversity between strata (Table 2.4) were not significant when all taxa were combined (Hotelling's $T^2 = 9.61$, df = 25, $P > 0.08$). Notably, cnidarians and amphipods were only present in seagrass sites. Differences between strata in the abundance for dominant taxa (>40% frequency of occurrence, i.e., nematodes, copepodes, polychaetes, oligochaetes, and bivalves) were significant (Hotelling's $T^2 = 23.75$, df = 25, $P < 0.024$); however, only the abundance of copepodes in seagrass samples was significantly higher than bare-sand sites in posterior tests (Tukey's test, df = 22, $P < 0.01$).

Discussion

Our results provide further evidence of the important role seagrass meadows play in terms of macrofaunal abundance and diversity, particularly providing essential nursery habitat for early life history stages of fishes and macroinvertebrates. Most notably, we found that crustaceans and fishes were seven and 20 times more abundant, respectively, in seagrass compared to adjacent bare-sand sites. Abundance and diversity were significantly higher on seagrasses for fishes and crustaceans. In addition, organisms of local economic importance, primarily juveniles, were commonly collected in the seagrass beds, most notably swimming crabs, penaeid shrimp, and fishes of the families Lutjanidae, Gerreidae, and Serranidae, which are of commercial importance and are captured for both sale and consumption by local fishermen.

Differences in the relative abundance of early life history stages among nearby habitat types is the most convincing evidence of the nursery function of a particular habitat type (Pearcy and Myers, 1973). By comparing our fish sizes, 80% of which were <40 mm SL, with literature values for size of maturity and maximum size of the same species, we concluded the majority (83%) of the seagrass specimens were early juvenile stages. This finding, together with the significantly higher fish abundance on seagrass sites, supports the hypothesis that seagrasses serve as nurseries for many Guatemalan fishes (Ogden and Gladfelter, 1983; Weinstein and Brooks, 1983; Pollard, 1984; Zieman and Zieman, 1989; Blaber et al., 1992).

Segrasses are reported to support small species with cryptic habits, while bare-substrate sites include adults of large mobile fish, or species gaining protection through schooling or by camouflage coloration (Bell and Pollard, 1989). In Australia, for example, a flounder capable of camouflaging itself on sand or mud is the most abundant species on unvegetated sites, whereas a small cryptic syngnathid fish is the typical seagrass resident (Connolly, 1994a). The only fish species we found on bare-sand sites was the shortchin stargazer, although they were almost equally abundant on seagrass sites. The shortchin stargazer's abundance on bare-sand sites is related to mouth and opercular adaptations that allow them to ventilate while buried in the sand with only their eyes exposed (Böhlke and Chaplin, 1968).

Our collection included seagrass fishes from both the warm-temperate and tropical zoogeographic zones. The dominance of members of the families Gerreidae, Haemulidae, and Scaridae, together with the reduced number of Sciaenidae, Engraulidae, and

Clupeidae indicated a transition from warm-temperate to tropical seagrass fish communities (Gilmore, 1987). Typical warm-temperate seagrass fishes such as the banded blenny, *Paraclinus fasciatus*, and the silver jenny, *Eucinostomus gula*, as well as tropical species like the Latin grunt were present in our samples. The dominance of grunts in seagrasses has been previously reported in Belize (Sedberry and Carter, 1993), Panama (Weinstein and Heck, 1979), and Rookery Bay, Florida (Sheridan, 1992). Moreover, post-larval grunts recruit to inshore environments dominated by seagrasses and mangroves (Ogden and Gladfelter, 1983). Although Latin grunts numerically dominated the seagrass fishes collected, they were present in only one sample in this study and further sampling (Arrivillaga, unpublished data) in the area has yielded only a few individuals. Juvenile grunts (primarily *Haemulon aurolineatum*) as well as grey snapper, *Lutjanus griseus*, are dominant fishes at a nearby artificial reef in Amatique Bay (Bortone et al., 1988). Otter trawling in deeper seagrass habitats in Bahia La Graciosa (Bortone, pers. com.) also documented the presence of juveniles and small adults of grunts, grey snapper, mojarras, syngnatids, and emerald parrotfish.

Biases related to different sampling techniques (Table 2.5) must be considered when interpreting and comparing results of various seagrass studies (Burchmore et al., 1984; Gilmore, 1990; Connolly, 1994b). Epibenthic resident seagrass fishes, such as labrids, gobiids, and syngnathids, have been widely reported as numerically dominant when efficient collecting devices such as drop nets, pop nets, or throw traps are used (Sogard et al., 1987; Gilmore, 1987). Species abundances and community composition on Guatemala's Atlantic coast were generally well characterized by our collecting method for

Table 2.5. Summary characteristics of fish studies in shallow seagrass systems. Comparative values from bare substrate sites within a study area are indicated in brackets []. Seagrass biomass is expressed in g dry wt · m^{-2} and fish density in individuals · m^{-2}.

Location	Seagrass species and biomass	Sampling technique	Mean density and range	Species · m^{-2}	Reference
Bahia La Graciosa, Guatemala	*T. testudinum* 45.5 - 132.3	Drop sampler (1.18 m^2)	4.53 (0 - 29.66) and [0.19 (0 - 1.69)]	1.92 [0.10]	Present study
Rookery Bay, Florida	*H. wrightii* dominated 5 - 18	Drop sampler (2.54 m^2)	5.85 (4.38-12.85) and [31.05 (2.54-95.73)]	- -	Sheridan, 1992
Florida Bay, Florida	*T. testudinum* 30 - 79.5	Throw trap (1 m^2)	8.55 (6.47 - 11.91)	- -	Sogard et al., 1987
Florida Bay, Florida	*T. testudinum* 27.6 - 79.5	Throw trap (1 m^2)	12.77 (8.33 - 47.68)	- -	Sogard et al., 1989
Tampa Bay, Florida	*T. testudinum*	Drop net (1 m^2)	~ 15 and [1.74]	3.6	Fonseca et al., 1996
New South Wales, Australia	*Posidonia australis*	Block net (400 m^2)	0.56 (0.42 - 0.73)	0.06	Burchmore et al., 1984
Indian River Lagoon, Florida	*H. wrightii* 1.41 - 6.83	Bag seine net (6 x 1.8 m)	1.85 (0.38 - 4.45)	0.003	Brown-Peterson et al., 1993
Gazi Bay, Kenya	*Thalassodendron ciliatum* dominated	Beach seine net	1.085 (0.59 - 1.58)[1] and [0.18]	0.49 [0.009]	De Trooch et al., 1996

[1] Value is geometric mean and range includes values of two seagrass areas.

all but the largest fishes. The absence of pelagic species (Clupeidae, Engraulidae, Exocetidae, Belonidae and Atherinidae) in studies using throw traps or drop samplers may be due, as Sogard et al. (1987) pointed out, to the tendency of these methods to capture only those pelagic species with a behavioral response of diving into seagrass beds when disturbed (e.g., pinfish, mojarras, and juvenile snappers and grunts).

The most comparable study to date (Sheridan, 1992) was conducted in Rookery Bay, Florida, with a drop sampler (Table 2.5). On two of four sampling dates, Sheridan (1992) found significantly higher fish densities in open-water than in seagrass habitat types, an unexpected result. Moreover, his seagrass sites were dominated by shoal grass, a seagrass species with narrow blades and a low leaf-surface-area index, supporting lower animal biomass and species diversity than seagrasses such as eel grass and turtle grass (Orth et al., 1984; Stoner, 1983). Similar natant macrofaunal densities can also be found in seagrass and adjacent non-vegetated sites when high water turbidity provides protection from predators, nullifying the attraction of seagrasses as shelter sites (Bell and Pollard, 1989); however, no turbidity data are available to qualify its effect in Sheridan's (1992) study.

Other seagrass studies have used a variety of gear types (Table 2.5) to document fish abundance and diversity. Sogard et al. (1987) used a throw trap in Florida Bay turtle grass meadows and found fish densities slightly exceeding our values from Guatemala. In later throw trap sampling in Florida Bay seagrasses, Sogard et al. (1989) found an extremely high fish density ($47.68 \cdot m^{-2}$), which was associated with high seagrass litter accumulation. Similarly, fish densities in Tampa Bay, Florida, sampled with a drop net

(Fonseca et al., 1996b), were higher in seagrass than bare sites. Fish densities in Guatemala's seagrasses were higher than those found by Brown-Peterson et al. (1993) who used a seine on *Halodule* beds in Indian River Lagoon, Florida. Observed differences may be primarily attributed to lower *Halodule* biomass, as well as to the difference in sampling gear. Also, using a block net, Burchmore et al. (1984) found fish densities and species diversity below our values (Table 2.5) in beds of *Posidonia australis*. Finally, seining in Kenya (De Trooch et al., 1996) and Australia (Gray et al., 1996; West and King, 1996) found higher fish densities and species diversity in seagrass than in unvegetated sites, comparable to our results.

Fish species composition and abundance in previously reported seagrass studies from Panama and Florida are generally concordant with our results. There was a high similarity of fish species (56.3% in common) between our study and in the Panamanian Caribbean (Weinstein and Heck, 1979). In Panama, absence of species like stargazers, toad fishes, and gobies may be attributed to the otter trawl sampling method, which has a limited efficiency collecting small organisms (Gilmore, 1990). Densities of spotfin mojarra, grey snapper, grunt, and frillfin goby, *Bathygobius soporator*, reported for Rookery Bay, Florida, seagrasses are similar to those found in Guatemala (Table 2.2). Sogard et al. (1989) reported mean densities of 0.159 individuals·m^{-2} for *Eucinostomus* spp. in seagrass sites in Florida Bay, a value close to our combined *E. argenteus* and *E. gula* abundance (0.22 individuals·m^{-2}). Banded blenny mean abundance in northwest Florida Bay was 0.13 individuals·m^{-2} (Sogard et al., 1989), a value that matches exactly our seagrass density for that species.

Decapod crustaceans constitute an important fish forage base in seagrass meadows where their abundance often exceeds that found on bare substrate sites (Lewis, 1984; Heck and Weinstein, 1989; Sheridan, 1992). Consistent with our results, Sheridan (1992) found significant habitat-related differences in Rookery Bay shrimp abundance, with higher densities in seagrass than in open-water sites; however, shrimp densities in Guatemala seagrasses (2.96 individuals·m^{-2}) were lower than the minimum shrimp abundances reported for Rookery Bay in either seagrass or open-water sites. Notably, Sheridan (1992) reports significantly higher densities of banded snapping shrimp, *Alpheus armillatus*, in open-water sites than in seagrass sites; however, in Guatemala, we collected them in seagrass, but not in bare-sand sites, with no apparent explanation for this pattern. Finally, decapod crustaceans in Panama turtle grass meadows (Heck, 1977) are dominated by the caridean shrimp, *Tozeuma carolinense*, a species not found in our sampling; however, other common species in Panama such as pink shrimp, and a majid crab, *Microphrys bicornutus*, were also abundant in Guatemala. The absence of grass shrimp, the most abundant species in Guatemala, in the Panama study, may be explained by the proximity of coral reefs (Heck, 1977).

Dana swimming crab densities were higher in seagrass than in bare-sand sites in Guatemala (0.45 and 0.26 individuals·m^{-2}, respectively) as blue crab are in Rookery Bay, Florida (2.15 and 0.77 individuals·m^{-2}, respectively). Higher abundances in seagrass sites have been related to the nursery value of seagrasses to blue crabs (Heck and Thoman, 1984), and in this case all Dana swimming crabs collected were juveniles. Perkins-Visser et al. (1996) report seagrasses as enhancing both survival and growth of blue crabs

through reduced cannibalism resulting from higher food abundance and from protection during molting. *C. danae* has been reported to rank in abundance from 9 to 19 in four sites, among all invertebrate species collected with an otter trawl in Panama's Caribbean seagrass meadows (Heck, 1977).

The lack of significant differences in the abundance of gastropods in seagrass versus bare-sand sites suggests that seagrass cover may not play an important role in their distribution. Young and Young (1982) reported no clear-cut seagrass effect on densities and number of species of gastropods and polychaetes compared to bare sand in Belize. Intense predation pressure was proposed by Young and Young (1982) as the primary regulating mechanism for gastropods abundance; however, Brown and Lodge (1993) found the abundance and diversity of invertebrates in vegetated habitat types to be explained by the amount of colonizable surface area and not predation risk.

We examined meiofauna densities as a possible explanation to the patterns observed in fish and macroinvertebrate abundances in seagrass and bare-sand sites in terms of food availability, as meiofauna, particularly harpaticoid copepods, form an important fraction of fish diets in seagrass (Bell et al., 1984). Total meiofauna densities are significantly higher in barren than on seagrass sites in Big Pine Key, Florida (Decho et al., 1985), whereas we were unable to detect significant differences. The absence of significant differences, other than for copepods, may be attributable to the coarse taxonomic levels used in our analysis, as species-level tests might be more discriminating. The dominance of nematodes in our samples concur with previous seagrass meiofauna studies (Fleeger and Chandler, 1983; Bell et al., 1984; Decho et al., 1985), and our

nematode and copepod abundance values in seagrass sites correspond with those reported from Tampa Bay, Florida (Bell et al., 1984).

The quality and quantity of habitat provided by seagrasses varies with environmental conditions (e.g., depth, substrate, wave energy, nutrient and light availability). Seagrass biomass and the index of leaf surface area have been identified as key organizing factors in macrophyte-associated faunal assemblages (Lewis, 1984). Sites of greater seagrass cover are associated with higher epibenthic invertebrate species diversity and abundance (Heck and Wetstone, 1977; Heck and Orth, 1980; Lewis, 1984; Orth et al., 1984). Seagrass leaf biomass and surface-area index values for shallow, high-energy sites in Guatemala's Atlantic coast were similar to previous turtle grass descriptions (Table 2.5), and corresponded with those of localities in Florida, Belize, and the Mexican and Honduran Caribbean (biomass range = 20.5 to 150.0 g dry wt·m^{-2}; leaf surface area index range = 0.40 to 3.23 $m^2 \cdot m^{-2}$) (Tomasko and Lapointe, 1991). While other studies (Lewis, 1984; Zieman and Zieman, 1989) report seagrass biomass values above those we found on sandy substrate, further sampling near the study area (Arrivillaga, unpublished data) found comparable biomass values associated with muddy substrates in lower wave energy sites (mean = 165.55 g dry wt·m^{-2}). Plant surface area has also been identified as an indicator of the extent of habitat structure provided by seagrasses (Virnstein, 1987), and in laboratory experiments, surface area estimates structural complexity better than plant biomass (Stoner, 1980). Our leaf surface area index estimates, recorded in shallow, high-energy sites, were similar to those reported

(Sogard et al., 1987) for turtle grass beds in Florida Bay (0.56 to 1.22 $m^2 \cdot m^{-2}$), but below estimates from other studies (Fonseca et al., 1996a).

We found significantly higher abundance and diversity of fish and crustacean faunas in seagrasses compared to bare-sand sites. Our results also documented the value of shallow-water seagrasses in terms of quality nursery areas for important commercial and forage species in Guatemala's Atlantic coast. This information should encourage resource managers and conservation agencies to conserve seagrass meadows from future coastal developments that can harm the health of these productive environments. Future research will focus on comparisons with nearby low-energy *T. testudinum* meadows on muddy substrates to examine differences in faunal abundance and composition, as well as the effect of seasonal environmental changes in the dynamics of seagrass faunas on Guatemala's Atlantic coast.

Summary

We describe the diversity and abundance of fishes and macroinvertebrates inhabiting sandy, shallow water seagrass and adjacent bare-sand sites near Bahia La Graciosa, on the Atlantic coast of Guatemala, to assess the relative importance of turtle grass (*Thalassia testudinum*) meadows as nurseries. Twenty-six samples (13 on each strata) were collected with a cylindrical drop sampler (1.18 m^2) during 14-17 December 1993. Microhabitat data, including mean depth, water temperature, turbidity, mid-water column velocity, distance to the shore, substrate percent sand content, salinity, dissolved oxygen concentration, and percent of the bottom covered by seagrass were recorded. Means for seagrass coverage, biomass, and leaf surface area index were 79.6%, 44.2 g dry

wt·m^{-2}, and 1.1 m^2·m^{-2}, respectively, on seagrass sites. Total crustacean and fish abundances were significantly higher ($P < 0.01$) by a factor of seven and 20 times, respectively, on seagrasses than on bare-sand sites, but no significant differences ($P > 0.05$) were detected for gastropods. The species diversity and evenness of fishes and crustaceans were both also significantly higher ($P < 0.01$) in seagrass samples. Seagrass fishes included 19 species and were numerically dominated by juvenile *Haemulon steindachneri*. The only fish present in bare-sand sites was *Dactiloscopus poeyi*, which was second in overall abundance. Other abundant seagrass fishes were *Nicholsina usta* and *Halichoeres pictus*. The most abundant crustacean species was the hermit crab, *Pagurus critinicornis*, followed by the longtail grass shrimp, *Periclimenes longicaudatus*, and the marsh grass shrimp, *Palemonetes vulgaris*. The dominant gastropod species was *Nassarius polygonatus*, followed by *Nerita virginica* and *Jaspidella jaspidea*. The size of seagrass fishes ranged from 12 to 69 mm standard length, and the majority (83%) were early juveniles, supporting the hypothesis of seagrasses as an important nursery for fishes.

References

Allen, G.R. 1987. Synopsis of the circumtropical fish genus *Lutjanus* (Lutjanidae). Pages 33-87 *in* J. J. Polovina and S. Ralston, eds. Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder, Colorado. 659 p.

Anderson, W.D. Jr. 1987. Systematics of the fishes of the family Lutjanidae (Perciformes: Percoidei), the snappers. Pages 1-33 *in* J. J. Polovina and S. Ralston, eds. Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder, Colorado. 659 p.

Baltz, D.M. 1990. Autoecology. Pages 585-607 *in* C.B. Schreck and P.B. Moyle, eds. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Baltz, D.M., C. Rakocinski and J.W. Fleeger. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. Env. Biol. Fish. 36: 109-126.

Bell, J.D. and D.A. Pollard. 1989. Ecology of fish assemblages and fisheries associated with seagrasses. Pages 565-609 *in* A. W. D. Larkum, A. J. MacComb and S. A. Shepherd, eds. Biology of seagrasses. Aquatic Plant Studies 2. Elsevier, Amsterdam.

Bell, J.D., D.J. Ferrell, S.E. McNeill, and D.G. Worthington. 1992. Variation in assemblages of fish associated with deep and shallow margins of the seagrass *Posidonia australis*. Mar. Biol. 114: 667-676.

Bell, S.S., K. Walters and J.C. Kern. 1984. Meiofauna from seagrass habitats: a review and prospectus for future research. Estuaries 7: 331-338.

Blaber, S.J.M., D.T. Brewer, J.P. Salini, J.D. Kerr, and C. Conacher. 1992. Species composition and biomasses of fishes in tropical seagrasses at Groote Eylandt, Northern Australia. Est. Coast. Shelf Sci. 35: 605-620.

Böhlke, J. E. and C. C. G. Chaplin. 1968. Fishes of the Bahamas and adjacent tropical waters. University of Texas Press, Austin, Texas. 771 pp.

Bortone, S. A., R. L. Shipp, W. P. Davis and R. D. Nester. 1988. Artificial reef development along the Atlantic coast of Guatemala. Northeast Gulf Sci. 10: 45-48.

Brown, K. M. and D. M. Lodge. 1993. Gastropod abundance in vegetated habitats: the importance of specifying null models. Limnol. Oceanogr. 38: 217-225.

Brown-Peterson, N. J., M. S. Peterson, D. A. Rydene and R. W. Eames. 1993. Fish assemblages in natural versus well established recolonized seagrass meadows. Estuaries 16: 177-189.

Bulthuis, D. A. 1990. Leaf surface area. Pages 69-70 *in* R. C. Phillips and C. P. McRoy, eds., Seagrass Research Methods, Chapter 11, UNESCO, Paris.

Burchmore, J. J., D. A. Pollard, and J. D. Bell. 1984. Community structure and trophic relationships of the fish fauna of an estuarine *Posidonia australis* seagrass habitat in Port Hacking, New South Wales. Aquat. Bot. 18: 71-87.

Connolly, R. M. 1994a. A comparison of fish assemblages from seagrass and unvegetated areas of a Southern Australian estuary. Aust. J. Mar. Freshwater Res. 45: 1033-44.

Connolly, R. M. 1994b. Comparison of fish catches from a buoyant pop net and a beach seine net in a shallow seagrass habitat. Mar. Ecol. Prog. Ser. 109: 305-309.

Decho, A. W., W. D. Hummon and J. W. Fleeger. 1985. Meiofauna-sediment interactions around subtropical seagrass sediments using factor analysis. J. Mar. Res. 43: 237-255.

De Troch, M., J. Mees, I. Papadopoulos and E. O. Wakwabi. 1996. Fish communities in a tropical bay (Gazi Bay, Kenya): seagrass beds vs unvegetated areas. Neth. J. Zool. 46: 236-252.

Fisher, W. (Ed.). 1978. FAO species identification sheets for fishery purposes. Western Central Atlantic (fishing area 31). Vols. 1-7.

Fleeger, J. W. and G. T. Chandler. 1983. Meiofauna responses to an experimental oil spill in a Louisiana salt marsh. Mar. Ecol. Prog. Ser. 11: 257-264.

Fonseca, M. S., D. L. Meyer and M. O. Hall. 1996a. Development of planted seagrass beds in Tampa Bay, Florida, USA .I. Plant components. Mar. Ecol. Prog. Ser. 132:127-139.

Fonseca, M. S., D. L. Meyer and M. O. Hall. 1996b. Development of planted seagrass beds in Tampa Bay, Florida, USA .II. Faunal components. Mar. Ecol. Progr. Ser. 132:141-156.

Gilmore, R. G. 1987. Subtropical-tropical seagrass communities of the Southeastern United States: fishes and fish communities. Fla. Mar. Res. Pub. 42: 117-137.

Gilmore, R. G. 1990. Nekton: biomass and abundance. Pages 129-136 *in* R. C. Phillips and C. P. McRoy, eds. Seagrass Research Methods, UNESCO, Paris.

Gray, C. A., D. J. McElligott and R. C. Chick. 1996. Intra- and inter-estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. Mar. Freshwater Res. 47: 723-35.

Heck, K. L. Jr. 1977. Comparative species richness, composition and abundance of invertebrates in Caribbean seagrass (*Thalassia testudinum*) meadows (Panama). Mar. Biol. 41: 335-348.

Heck, K. L. Jr. and G. S. Wetstone. 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. J. Biogeogr. 4: 135-142.

Heck, K. L. Jr. and R. J. Orth. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. Pages 449-464 *in* V. S. Kennedy, ed. Estuarine perspectives, Academic Press, New York.

Heck, K. L. Jr. and T. A. Thoman. 1984. The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. Estuaries 7: 70-92.

Heck, K. L. Jr. and M. P. Weinstein. 1989. Feeding habits of juvenile reef fishes associated with panamanian seagrass meadows. Bull. Mar. Sci. 45: 629-636.

Heck, K. L. Jr. and L. B. Crowder. 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. Ch. 14: 281-295 *in* S. S. Bell, E. D. McCoy and H. R. Mushinsky, eds. Habitat Structure: The physical arrangements of objects in space. Chapman and Hall, New York. 434 pp.

Johnson, R. A. and D. W. Wichern. 1992. Applied multivariate statistical analysis. Prentice Hall, New Jersey. 642 pp.

Kikuchi, T. and Perez, J. M. 1977. Consumer ecology of seagrass beds. Pages 147-194 *in* C. P. McRoy and C. Helfferich, eds. Seagrass Ecosystems: A Scientific Perspective. Marcel Edkker Inc. New York.

Lewis, F. G. III. 1984. Distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule* and bare sand substrata. Mar. Ecol. Prog. Ser. 19: 101-113.

Littel, R. C., R. J. Freund and P. C. Spector. 1991. SAS System for linear models. Third Edition, SAS Institute Inc. Cary, NC. 329 pp.

Livingston, R. J., R. S. Loyd and M. S. Zimmerman. 1976. Determination of sampling strategy for benthic macrophytes in polluted and unpolluted coastal areas. Bull. Mar. Sci. 26: 569-575.

Lubbers, L., W. R. Boynton and W. M. Kemp. 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. Mar. Ecol. Prog. Ser. 65: 1-14.

Margalef, R. 1968. Perspectives in ecological theory. University of Chicago Press. Chicago.

Middleton, M. J., J. D. Bell, J. J. Burchmore, D. A. Pollard and B. C. Pease. 1984. Structural differences in the fish communities of *Zostera capricorni* and *Posidonia australis* seagrass meadows in Botany Bay, New South Wales. Aquat. Bot. 18: 98-109.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons. New York. 547 pp.

Ogden, J. C. 1980. Faunal relationships in Caribbean seagrass beds. Pages 173-198 *in* R. C. Phillips and C. P. McRoy, eds. Handbook of seagrass biology: an ecosystem perspective. Garland STPM Press, New York.

Ogden, J. C. and Gladfelter, E. H. eds. 1983. Coral reefs, seagrass beds and mangroves: their interaction in the coastal zones of the Caribbean. Unesco Reports in Marine Science, 23. Montevideo, Uruguay. 133 pp.

Orth, R. J., K. L. Heck Jr. and J. van Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7: 339-350.

Orth, R. J. 1992. A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. Pages 147-164 *in* D. M. John, S. J. Hawkins, and J. H. Price, eds. Plant-Animal Interactions in Marine Benthos. The Systematics Association Special Volume No. 46. Clarendon Press, Oxford.

Ott, J. A. 1990. Biomass. Pages 55-60 *in* R. C. Phillips and C. P. McRoy, eds. Seagrass Research Methods, Chapter 8, UNESCO. Paris.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. TREE, 10: 430.

Pearcy, W.G., and S.S. Myers. 1974. Larval fishes of Yaquina Bay, Oregon: a nursery ground for marine fishes? Fish. Bull. 72: 201-213.

Pergent, G., V. Rico-Raimondino, and C. Pergent-Martini. 1997. Fate of primary production in *Posidonia oceanica* meadows on the Mediterranean. Aqua. Bot. 59: 307-321.

Perkins-Visser, E., T. G. Wolcott and D. L. Wolcott. 1996. Nursery role of seagrass beds: enhanced growth of juvenile blue crabs (*Callinectes sapidus* Rathbun). J. Exp. Mar. Biol. Ecol. 198: 155-173.

Pielou, E.C. 1966. The measurement of diversity in different types of biological collections. J. Theoret. Biol. 13: 131-144.

Pielou, E. C. 1975. Ecological diversity. Wiley-Interscience. New York.

Pollard, D. A. 1984. A review of ecological studies on seagrass-fish communities, with particular reference to recent studies in Australia. Aquat. Bot. 18: 3-42.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 367 pp.

Robertson, A. I. 1984. Trophic interactions between the fish fauna and macro benthos of an eelgrass community in Western Port, Victoria. Aquat. Bot. 18: 135-153.

Robertson, A. I. and Duke, N. C. 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. Mar. Biol. 96: 193-205.

Robertson, A. I., P. Dixon and P. A. Daniel. 1988. Zooplankton dynamics in mangrove and other nearshore habitats in tropical Australia. Mar. Ecol. Prog. Ser. 43: 139-150.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea and W. B. Scott. 1991. A list of common and scientific names of fishes from United States and Canada. American Fisheries Society, Special Publication No. 12. 174 pp.

Rozas, L. P. and Odum, W. E. 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. Oecologia 77: 101-106.

SAS Institute Inc. 1985. SAS user's guide: statistics. Version 5 Edition. Cary, NC: SAS Institute Inc. 941 pp.

Schlotzhauer, S. D. and R. C. Littell. 1987. SAS System for elementary statistical analysis. Cary, NC; SAS Institute Inc. 416 pp.

Sedberry, G. R. and J. Carter. 1993. The fish community of a shallow tropical lagoon in Belize, Central America. Estuaries 16: 198-215.

Sheridan, P. F. 1992. Comparative habitat utilization by estuarine macrofauna within the mangrove ecosystem of Rookery Bay, Florida. Bull. Mar. Sci. 50: 21-39.

Sogard, S. M., G. V. N. Powell and J. G. Holmquist. 1987. Epibenthic fish community on Florida Bay banks: relations with physical parameters and seagrass cover. Mar. Ecol. Prog. Ser. 40: 25-39.

Sogard, S. M., G. V. N. Powell and J. G. Holmquist. 1989. Spatial distribution and trends in abundance of fishes residing in seagrass meadows on Florida Bay mudbanks. Bull. Mar. Sci. 44: 179-199.

Stoner, A. W. 1980. Perception and choice of substratum by epifaunal amphipods associated with seagrasses. Mar. Ecol. Progr. Ser. 3: 105-111.

Stoner, A. W. 1983. Distributional ecology of amphipods and tanaidaceans associated with three sea grass species. J. Crust. Biolo. 3: 505-518.

Tomasko, D. A. and B. E. Lapointe. 1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: field observation and experimental studies. Mar. Ecol. Prog. Ser. 75: 9-17.

Virnstein, R. W. 1987. Seagrass associated invertebrate communities of the Southeaster U.S.A.: a review. Fla. Mar. Res. Pub. 42: 90-115.

Weinstein, M. P. and K. L. Jr. Heck. 1979. Ichthyofauna of seagrass meadows along the Caribbean coast of Panama and in the Gulf of Mexico: composition, structure and community ecology. Mar. Biol. 50: 97-107.

Weinstein, M. P. and Brooks, H. A. 1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: community composition and structure. Mar. Ecol. Prog. Ser. 12: 15-27.

West, R. J. and R. J. King. 1996. Marine, brackish, and freshwater fish communities in the vegetated and bare shallows of an Australian coastal river. Estuaries 19: 31-41.

Young, D. K. and M. W. Young. 1982. Macrobenthic invertebrates in bare sand and seagrass (*Thalassia testudinum*) at Carrie Bow Cay, Belize. In: K. Rutzler and I. G. Macintyre eds., The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, 1: Structure and communities. Smithson. Contrib. Mar. Sci. 12: 115- 126.

Zieman, J. C., Macko, S. A. and Mills, A. L. 1984. Role of seagrasses and mangroves in estuarine food webs: temporal and spatial changes in stable isotope composition and amino acid content during decomposition. Bull. Mar. Sci. 35: 380-392.

Zieman, J. C. and Zieman, R. T. 1989. The ecology of the seagrass meadows of the west coast of Florida: a community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85: 155 pp.

Zimmerman, R. J., T. J. Minello, and G. Zamora. 1984. Selection of vegetated habitat by *Penaeus aztecus* in a Galveston Bay salt marsh. Fish. Bull. 82: 325-336.

CHAPTER 3

FISH AND DECAPOD CRUSTACEAN COMMUNITY STRUCTURE IN EXPOSED AND PROTECTED SEAGRASS ENVIRONMENTS ON THE ATLANTIC COAST OF GUATEMALA

Introduction

Differences in seagrass bed characteristics, related to degree of exposure to wave action and resulting in differences in substrate type, may also result in differential patterns of fish and decapod crustacean community structure and habitat utilization. The effect of hydrodynamic regimes on seagrass structure has been observed (Fonseca and Bell, 1998), as well as the role of seagrasses in altering water column velocity and waves (Fonseca et al., 1983; Fonseca and Cahalan, 1992). Many studies, mostly in temperate areas, have explored the effect of exposure to tidal currents and wave energy on seagrass faunal abundance and composition. Areas with higher tidal currents are reported to have higher numbers of macrobenthic species associated with turtle grass *Thalassia testudinum* in Biscayne Bay, Florida (O'Gower and Wacasey, 1967). Sediment stability, resulting from dense seagrass stands, results in higher infaunal diversity and density on eelgrass *Zostera marina* beds in Chesapeake Bay and turtle grass beds in Bermuda (Orth, 1977). Degree of exposure, eelgrass coverage, and sediment structure are the primary factors affecting the composition and quantity of mobile epibenthic fauna in the Swedish west coast (Phil,1986). Significant variations in shrimp density in high-energy patchy and low-energy continuous shoalgrass *Halodule wrightii* beds occur in North Carolina, USA (Murphey and Fonseca, 1995). Eelgrass and shoalgrass beds effect sediment stability and clam growth (Irlandi, 1996) in high energy sites and wave exposure and depth also effect

epiphyte dynamics (Pinckney and Micheli, 1998) off the coast of North Carolina. Wave energy may have an impact on seagrass epiphytes through abrasion and removal of attached diatoms, whereas cyanobacteria, which are typically smaller and more firmly attached, are less susceptible to abrasion. Similarly, patterns in sandy beach surf-zone fish communities show increasing abundance as wave energy decreases, and highest diversity and species richness at intermediate levels of exposure (Clark, 1997).

The study of diel effects on seagrass fauna has revealed contrasting results. Larger number of invertebrate fauna individuals are captured at night than during day on Panamanian turtle grass meadows (Heck, 1977), but no significant diel differences are found in epibenthic macroinvertebrate communities in sub-tropical manatee grass *Syringodium filiforme*, turtle grass, and shoalgrass on the northeast Gulf of Mexico (Greening and Livingston, 1982). In St. Croix, diel variations of the fish fauna on a *Thalassia*-dominated seagrass meadow corresponds to movements from diurnal resting sites in nearby coral reefs to feeding sites over seagrass at night (Robblee and Zieman, 1984), whereas diel cycles of seagrass banks habitats utilization by fish in Florida Bay are related to prey availability (Sogard et al., 1989). Patterns of penaeoid and caridean shrimp species composition and abundance are similar between day and night in turtle grass beds on the north coast of Puerto Rico (Bauer 1985a and b); however, diel patterns of fish and decapod crustacean immigration to artificial eelgrass units in New Jersey indicate higher immigration during night time (Sogard and Able, 1994). Finally, the diel changes in fish assemblages associated with an Australian eelgrass *Zostera capricorni* and bare sand in

two south-eastern Australia estuaries are consistently similar during day and night (Gray et al., 1998).

Seagrasses are important marine resources for fishes and decapod crustaceans on the Atlantic coast of Guatemala, and provide increased food and refugia for juvenile fish and crustaceans (Arrivillaga and Baltz, 1999). Seagrass meadows support highly diverse fish and macroinvertebrate communities around the world (Ogden, 1980; Heck and Orth, 1980; Orth, 1992), and are essential nursery areas for juvenile fishes, shrimp, and crabs (Ogden and Gladfelter, 1983; Weinstein and Brooks, 1983; Pollard 1984; Zieman and Zieman, 1989; Blabber et al., 1992; Connolly, 1994; Perkins-Visser et al., 1996). However, the importance of (abiotic) physico-chemical and biotic environmental factors such as exposure to wave action and seagrass characteristics on seagrass fauna of tropical environments remain unclear.

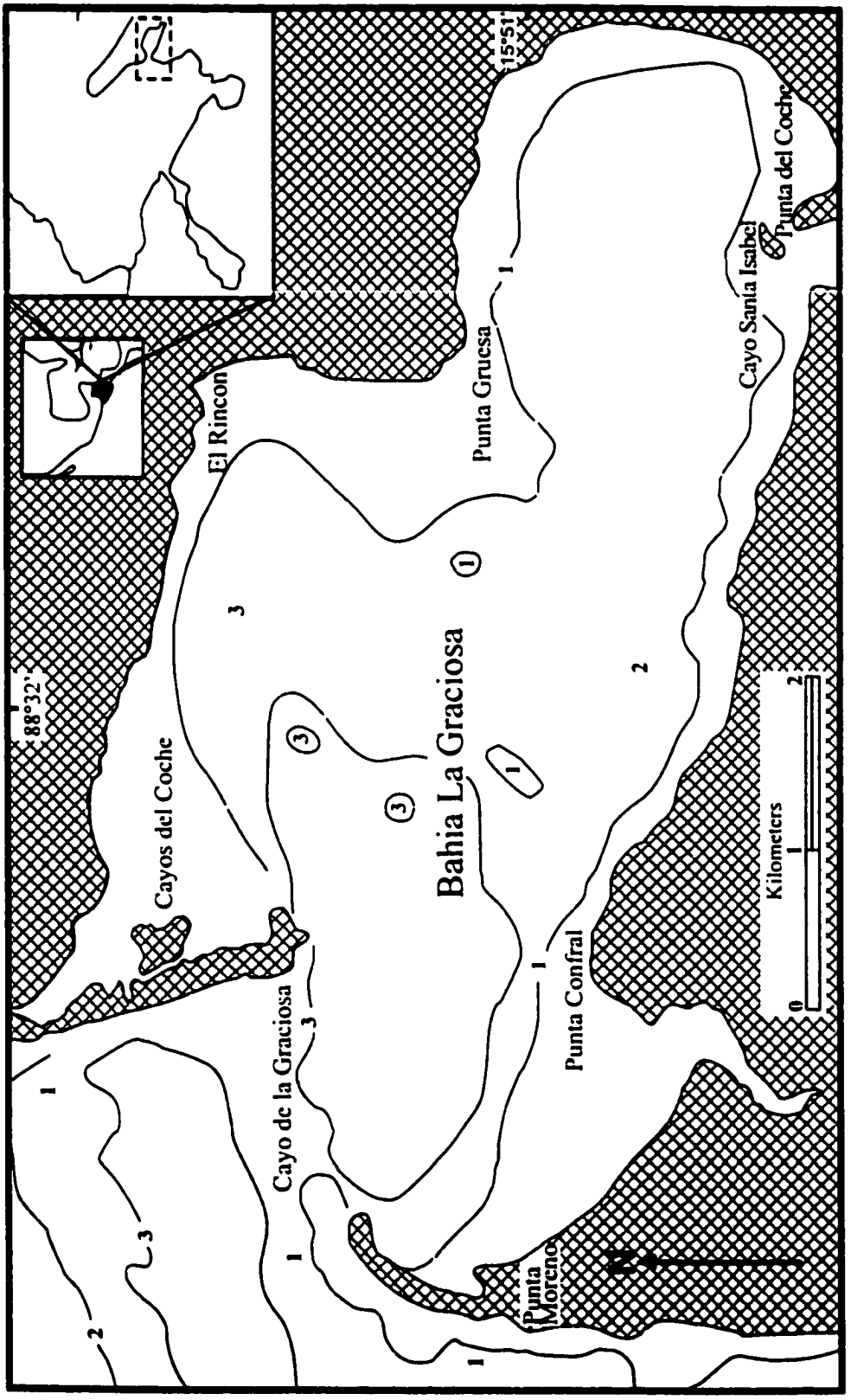
To analyze the influences of environmental factors, particularly degree of exposure to wave action, on the fish and decapod crustacean communities, we examined: (1) community structure between protected and exposed seagrass habitat types, (2) environmental variables between habitat types, (3) densities of common species, and (4) diel differences in species composition and abundance.

Materials and Methods

Study Area

Bahia La Graciosa is a shallow bay surrounded by a red mangrove *Rhyzophora mangle* forest, and is located on the Gulf of Honduras, on the Caribbean coast of Guatemala (Fig. 3.1). It supports extensive seagrass beds consisting mainly of turtle

Figure 3.1. Map of the study area, Bahia La Graciosa, Guatemala (depths in fathoms).



grass. Sandy substrates dominate the bay's mouth and surrounding area, whereas most of the interior bay is dominated by clay-silt substrates. The mean depth inside the bay is 2 m and at the mouth it is 1.5 m. The shallow, high wave energy conditions typical around the bay's mouth differ substantially from nearby seagrass meadows occurring inside the bay and characterized by lower energy levels. Tidal range in the study area is small with a maximum amplitude of 1 m. The primary freshwater influence in the region is from Rio Dulce, located on the western side of the Amatique Bay; however, direct precipitation into the Bahia La Graciosa drainage is also important. Rainfall occurs throughout the year (mean annual precipitation is 3.1 m) with a maximum monthly mean of 38.9 cm in October and a minimum monthly mean of 12 cm in March. The Atlantic coast of Guatemala, though only 200 km long, supports important commercial and artisanal fisheries.

Sample Collection and Analysis

Between 14-18 June 1994, we conducted a stratified random sampling survey of exposed (beach) and protected (bay) seagrass habitat types. Gross sediment composition, qualitative observations of current flow, and degree of exposure to wind-generated waves were used as initial habitat type classification characteristics. Five strata in each habitat type were identified and sampled equally. Individual sample sites within sectors were selected randomly and considered to be statistically independent. We used a cylindrical drop sampler that covered an area of 1.18 m^2 and consisted of a metal skirt and clear acrylic walls to reduce visual avoidance by nekton. The sampler was suspended from a boom extending 2 m beyond the bow of a small (6 m) boat and about 0.4 m above the water. A pull-pin release mechanism was used to drop the sampler on randomly selected

sites within sampling sectors in the range of depths covered by the sampler (0 - 1 m). Upon deployment, and after firmly setting the sampler, a seawater solution of powdered rotenone (5% cube') was applied, and the fishes and decapod crustaceans swimming to the surface were collected with dip nets. We then swept the entire basal area thoroughly with landing nets (Cummings Model 270-12", 5 mm mesh) to capture any remaining organisms. We continued sweeping until three successive passes yielded no organisms. This technique captures 96.5% of the nekton present (Duffy and Baltz, 1998). Small specimens were preserved directly in 95% ethanol, but larger organisms were preserved in a 10% buffered formalin solution, then transferred to 95% ethanol. Individuals were identified to species, counted, and measured to the nearest millimeter in standard length (SL for fishes), carapace width (CW for crabs), and carapace length (CL for shrimp). Common names were assigned according to Fisher (1978), Williams et al. (1988), and Robins (1991).

Sampling was designed to collect a similar number of samples in beach and bay habitat types over the full range of seagrass bottom coverage (0 - 100 %). A total of 71 samples were collected, including 32 samples in beach and 39 samples in bay habitat types. At each sampling site minimum and maximum depths, distance to the shore, substrate type (sand or mud), bottom visibility, turbidity in NTU (Monitek, model 21 PE portable nephelometer), mid-water-column velocity (Montedoro-Whitney model PVM-2A portable velocity meter), water temperature (pocket thermometer), salinity (temperature-compensated refractometer, AO model 10419), dissolved oxygen concentration (YSI dissolved oxygen meter Model 57), percent of the bottom covered by seagrass, and shore

vegetation, were recorded. Sixteen of the 71 samples were collected at night (7 and 9 in beach and bay sites, respectively) in an effort to evaluate diel changes in community structure. At night, the same procedures were followed, except that the general sampling areas were staked during the previous day to mark off areas with varying levels of seagrass coverage.

Seagrass biomass and leaf characteristics were estimated by collecting a 10 cm^2 core sample of the grasses to a substrate depth of 10 cm with each drop sample. Seagrass leaf biomass (g dry $wt \cdot m^{-2}$) included seagrass leaves (above-ground, green blades) dried in a 60 °C oven at to constant weight (Ott, 1990). We included any attached epiphytes and carbonate materials, but roots, rhizomes (short and long shoots), and drift algae were excluded (Sheridan, 1992). We also estimated the leaf surface area index (m^2 leaf area $\cdot m^{-2}$ substrate) from measurements of individual leaf length and width (above-ground, green blades) following Bulthuis (1990).

With each drop sample, a sediment sample was collected. In these samples, organic matter was oxidized with hydrogen peroxide and the remaining portion was analyzed for percent sand content by separating the sand and fine fractions and obtaining their respective dry weights (Buchanan, 1984; Gee and Bauder, 1986; Sheldrick and Wang, 1993).

For both environmental and faunal data sets, residuals of the MANOVA model were analyzed for normality with the Normal Procedure of SAS (Schlotzhauer and Littell, 1987). Where there was a lack of normality in the data sets, power transformations (x+1) (Johnson and Wichern, 1992) were used to achieve or approach normality before

comparing beach and bay samples. Hotelling's T^2 Test (Littell et al., 1991) was used to compare means of beach and bay environmental variables and densities (number·m^{-2}) of the 10 most common fish and decapod crustacean species, total fishes, and total crustaceans. Hotelling's T^2 is a multivariate test of H_0: $\mu=\mu_0$ where μ and μ_0 are vectors of response variable means from two populations, and its likelihood ratio is equivalent to the Wilk's lambda of a MANOVA with two populations (Johnson and Wichern, 1992). When overall significant differences between bay and beach means were detected with Hotelling's T^2, Least Squares Means (LSMeans) posterior tests ($\alpha = 0.05$, with the BonFerroni correction) were performed to identify means that differed significantly.

A rotated factor analysis of environmental data was used to describe the relationships among variables and reduce the number of environmental axes. Initial loadings were extracted by principal components analysis of the correlation matrix followed by varimax rotation (SAS Institute, 1989) to generate a more readily interpretable structure. Ideally, each variable loads heavily (> 0.50) on a single factor and has only small-to-moderate loadings on remaining factors (Johnson and Wichern, 1992). Factor scores were plotted in three dimensions to examine their distribution in environmental space. Centroids for both habitat types were plotted as spheres with radii representing two standard errors (calculated as the mean standard error of the first three factors) around the mean as a visual test of significant differences. Similarly, sample factor scores were used to explore species locations in environmental space. Centroids of the first three mean factor scores (± 2 SE) were used to identify the relative positions of species, along major environmental gradients (Grossman et al., 1991). Weighted means of

factor scores were calculated for each species based on species density per sample, and were plotted on three axes to identify major responses of faunal densities to environmental variables (Duffy and Baltz, 1998).

Multiple linear regression models were constructed to evaluate the relative roles of environmental variables (and their squared terms to identify non-linear responses) for predicting total fish and total crustacean densities. The models with the highest adjusted-r^2 were selected, guarding for model over-parametrization with Mallow's Cp (Neter et al., 1990). Models with all samples as well as blocking by habitat type were evaluated.

We examined cumulative diversity plots to determine if we had adequately characterized faunal groups with our sampling effort, to estimate the community diversity (H'_{pop}, *sensu* Pielou, 1966), and to compare community diversity between beach and bay habitat types. Cumulative sample diversity was calculated in steps after pooling in sequence randomly selected samples until all samples were included. This procedure was repeated 50 times and means were obtained for each sample addition step. These means were used to fit negative exponential growth functions using a non-linear regression procedure (SAS Institute Inc. 1985). The model parameters [$H'_C = H'_A * (1-\exp(-k * (x-x_0)))$, where H'_C = cumulative diversity, H'_A = asymptotic cumulative diversity, k = exponential change rate, x = number of cumulative samples, and x_0 = theoretical number of cumulative samples corresponding to $H'_C = 0$] were used to calculate predicted values and they were plotted together with the cumulative diversity step means and visually examined to determine whether or not they approached an asymptote. The point at which cumulative-diversity-step means approached an asymptote (t in Pielou, 1966) was

identified as the number of cumulative samples that resulted in less than a 10% increase in cumulative diversity (Mueller-Dombois and Ellenberg, 1974). Using this value, we estimated the community diversity (H'_{pop}) and its sampling variance (Pielou, 1966). Community diversity comparisons between habitat types for a faunal group were considered significantly different if the 95% confidence intervals (CI) for H'_{pop} did not overlap.

To test for differences in fish and decapod crustacean community structures between beach and bay habitat types, we used two different approaches. First, concordance in community structure was estimated with Spearman's Rank Correlation test (Herbold, 1984). Correlations due to rarity were reduced by examining only the 10 most abundant species of fishes and decapod crustaceans, respectively. We calculated rank densities, and tested the null hypothesis of no concordance in community structure between habitat types. The use of ranks contributes a substantial conservative bias when comparing collections that vary greatly in the number of individuals present. If species ranks were significantly correlated we assumed that community structure was similar between beach and bay samples (Grossman, et al. 1982). In the second approach, we tested for significant differences in species composition between habitat types with another non-parametric procedure, ANOSIM (analysis of similarities), applied to the similarity matrix of species-by-samples with the PRIMER statistical package (Carr, 1997). ANOSIM is a Mantel-type permutation test combined with a general randomization approach to generate significance levels (Monte Carlo tests), analogous to a multivariate analysis of variance (MANOVA) (Clarke and Green, 1988; Clarke, 1993; Clarke and

Warwick, 1994). Briefly, this method computed a test statistic reflecting the observed ranked similarities between samples in groups selected *a priori* (here beach and bay habitat types), contrasted with similarities among replicates from different groups. Where rW is the average of all rank similarities among replicates within habitat types, and rB is the average of rank similarities from all pairs of replicates between different habitat type. The test statistic is $R = (rW - rB) / (M/2)$, where $M = n(n-1)/2$, and n is the total number of samples under consideration. R will usually fall between zero and one, although its value ranges from -1 to +1. R is equal to one only if all replicates of each habitat type are more similar to each other than any replicates from different habitat types. R is approximately zero when the null hypothesis is true and similarities among and within habitat types are the same on average. Next, the statistic is re-computed under permutations of the sample identification labels. Under the null hypothesis H_0: 'no differences between habitat types' there will be little effect on the average value of R if the labels identifying which replicates belong to which habitat type are arbitrarily re-arranged. This process is repeated a large number of times (20,000 simulations in this study). Finally, the significance level is calculated by referring the observed value of R to its permutation distribution. If H_0 is true, the likely spread of values of R is given by the random rearrangement. When the true value of R was unlikely to have come from this distribution, we rejected the null hypothesis. Formally, if only t of the T simulated values of R are as large (or larger than) the observed R, then H_0 can be rejected at a significance level of $100\ (t+1)/(T+1)\%$. Using this technique, we tested the null hypothesis of no significant differences in community composition between beach and bay habitat types. Similarity matrixes, used to

compute the R value in ANOSIM, were based on the Bray-Curtis similarity measure, and consisted of all samples containing fish or decapod crustacean minus those samples identified as outliers (63 and 57 samples out of 71 total samples were included in the fish and decapod crustacean analyses, respectively). Also for this analysis, all singleton and unique species were eliminated from the data set, giving a more conservative community composition. A total of 16 fish and 15 decapod crustacean species (89.8 and 83.8 % of fish and crustaceans, respectively) were included.

Diel variations in community structure were assessed by ANOSIM models and by contrasting species densities between day and night samples. We used a two-way crossed ANOSIM with habitat type (beach and bay) and time (day and night), followed by a one-way ANOSIM to compare all pair-wise combinations of factors (day-beach, night-beach, day-bay, and night-bay) when significant differences were found for the main factors. Analyses were performed separately for fish and decapod crustacean species, but only the ten most common species were tested to eliminate similarities due to rarity. All samples that included fishes or decapod crustaceans were included (65 and 62 samples, respectively). Densities of total fishes, total crustaceans, and the ten common species form each group were compared between day and night in beach and bay habitat type sites. We used two-way factorial MANOVA models (main factors time and habitat type and their interaction), followed by Least Squares Means comparisons when significant differences were found. The null hypotheses were no significant differences in community structure and species densities between day and night samples.

Results

A total of 71 samples were collected, including 32 samples in beach and 39 samples in bay habitat types. Of the 71 samples, sixteen were collected at night.

Environmental Variables

Hotelling's T^2 test indicated overall significant differences (T^2 value = 709.51, df = 70, $P < 0.0001$) between beach and bay habitat types in environmental variables. Significant differences were found (LSMeans, df = 70, $P < 0.05$) for all variables except salinity and percent of bottom covered by seagrass (Table 3.1). Physico-chemical differences reflect actual differences between habitat types, especially depth profile, water quality, and exposure. These differences were also reflected in seagrass characteristics, most notably biomass and leaf area index. Bay samples had 1.6 times higher seagrass biomass and 2.2 times higher leaf area than beach samples, clearly indicating a more developed seagrass bed structure in the protected habitat type.

In the factor analysis, five factors had eigenvalues ≥ 1 and explained 79.6% of environmental variance (Table 3.2). Factor one represented all seagrass variables (leaf biomass, leaf area, and percent of bottom covered by seagrass) and explained 23.7% of the total variance. Factor two represented major habitat type differences (percent sand, distance from shore, turbidity, and water depth) and explained 22.4% of the total variance. Factor three included temperature and dissolved oxygen and explained 12.3% of total variance. Factor four represented water velocity (11.3% of total variance), and Factor five represented salinity and explained 9.8% of the total variance. The plot of all samples in three-dimensional-environmental space (Fig. 3.2) revealed that most of the separation

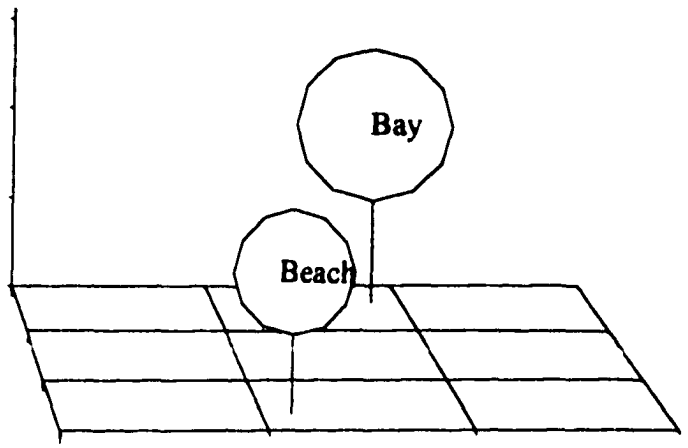
Table 3.1. Environmental data (Mean ± 1SE) for samples collected in exposed (beach) and protected (bay) seagrass habitat types in Bahia La Graciosa, Guatemala (12-18 June, 1994). Significant differences in means of physico-chemical variables between habitat types were detected (Hotelling's $T^2 = 709.51$, df = 70, $P < 0.0001$). In posterior testing (LSMeans, df = 70) p-values indicate significant differences between bay and beach samples.

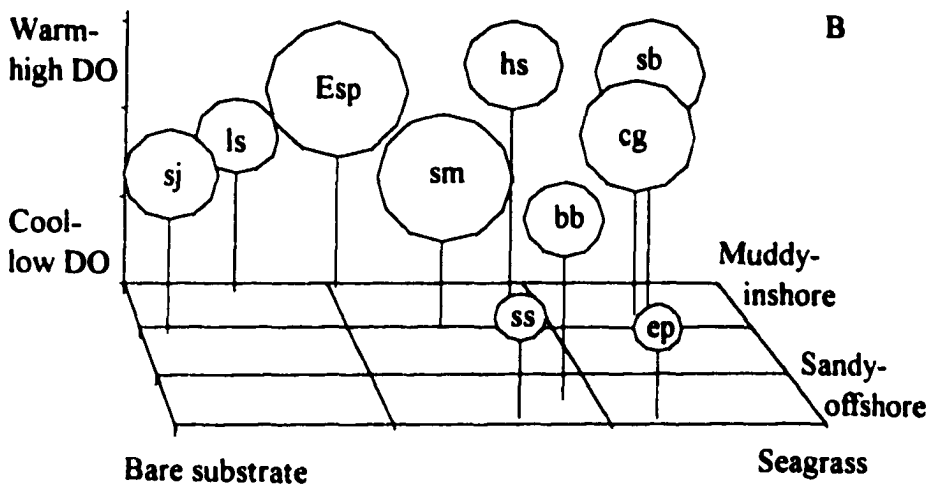
Variable	Beach	Bay	p-value	Combined
Depth (cm)	61.8 ± 3.23	72.8 ± 2.65	0.0128	67.9 ± 2.14
Distance to shore (m)	78.1 ± 12.18	7.4 ± 0.78	0.0001	39.2 ± 6.89
Substrate % sand content	97.8 ± 0.25	79.3 ± 2.60	0.0001	87.6 ± 1.80
Turbidity (NTU)	0.4 ± 0.07	1.7 ± 0.30	0.0001	1.1 ± 0.18
Current velocity ($cm \cdot s^{-1}$)	0.04 ± 0.01	0.01 ± 0.01	0.0153	0.02 ± 0.01
Temperature (°C)	30.8 ± 0.17	31.7 ± 0.18	0.0006	31.3 ± 0.14
Salinity (ppt)	27.3 ± 0.39	27.2 ± 0.71	0.5589	27.2 ± 0.42
Dissolved oxygen (ppm)	7.1 ± 0.22	6.2 ± 0.26	0.0020	6.6 ± 0.18
Seagrass				
Percent cover	59.2 ± 6.97	80.5 ± 5.75	0.0534	70.9 ± 4.60
Biomass ($g\ dw \cdot m^{-2}$)	83.3 ± 14.19	134.2 ± 18.19	0.0199	110.6 ± 12.08
Leaf area index ($m^2 \cdot m^{-2}$)	1.2 ± 0.19	2.6 ± 0.37	0.0008	2.0 ± 0.24
N	32	39		71

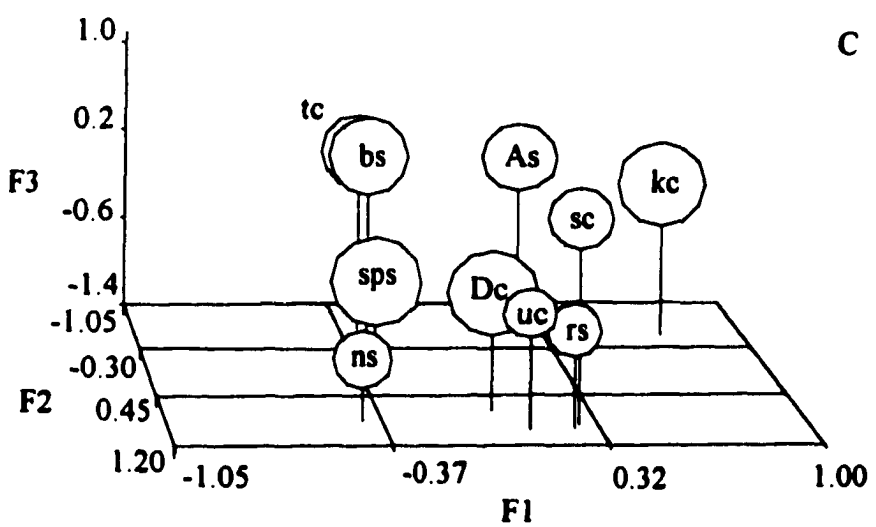
Table 3.2. **Rotated factor loadings (VARIMAX rotation over five axes) for the environmental variables measured in 71 samples in exposed (beach) and protected (bay) seagrass habitat types in Bahia La Graciosa, Guatemala (12-18 June, 1994). Numbers in boldface identify factors where variable scores are highest.**

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Leaf biomass	**0.9686**	-0.0004	0.0037	-0.0592	0.0077
Leaf area	**0.9356**	-0.1196	0.0285	-0.1388	-0.0261
Percent seagrass cover	**0.7933**	-0.0203	0.2057	0.0694	-0.0177
Substrate % sand content	-0.1889	**0.8188**	0.1604	0.0847	-0.1007
Distance	-0.0466	**0.7390**	-0.1740	0.4373	-0.0720
Turbidity	-0.0284	**0.6677**	-0.2330	0.0248	0.4120
Depth	-0.2948	**-0.5862**	0.1059	0.5460	0.1590
Temperature	0.2028	-0.2526	**0.8277**	-0.1382	0.0778
Dissolved Oxygen	0.0344	0.5734	**0.6825**	-0.0117	0.1010
Velocity	0.0057	0.2256	-0.1320	**0.8362**	-0.0914
Salinity	-0.0209	-0.0215	0.1304	-0.0567	**0.9208**
Variance explained	2.6112	2.4647	1.3500	1.2464	1.0839
% of total var. explained	23.74	22.41	12.27	11.33	9.85
Cumulative var. explained	23.74	46.14	58.42	69.75	79.60

Figure 3.2. a) Habitat type centroids for beach and bay environmental data in three-dimensional factor space. The radii of balloons estimate two standard errors around the centroids. b) Fish and c) decapod crustacean species plot of centroids for the common ten species of each group in three-dimensional factor space. Species name abbreviations are: As=American grass shrimp; bb=banded blenny; bs=banded snapping shrimp; cg=crested goby; Dc=Dana swimming crab; ep=emerald parrotfish; Esp=*Eucinostomus* sp.; hs=hardhead silverside; kc=knot-finger mud crab; ls=lined sole; ns=night shrimp; rs=rock shrimp; sb=seabream; sc=speck-claw decorator crab; sj=silver jenny; sm=spotfin mojarra; ss=shortchin stargazer; sps=southern pink shrimp; tc=truncate rubble crab; uc=urn crab.







between beach and bay samples occurred across factor two. Although bay samples tended to score higher than beach samples in factor one, samples from both habitat types encompassed the full range of seagrass coverage. Habitat type centroids and their confidence intervals indicated non-overlapping patterns of distribution with a clear separation of means for bay and beach samples (Fig. 3.2).

Fish Fauna

A total of 451 fish specimens were collected, representing 29 species in 23 families (Table 3.3). The most important families were Gerreidae and Labrisomidae, represented by three species each, and Sciaenidae and Batrachoididae, represented by two species each. Nineteen other families were represented by one species only. Overall, the most abundant species was the spotfin mojarra, accounting for 28.6% of all fishes, followed by larval Eucinostomus sp., accounting for 16.6% of all fishes. These two species were first and third, respectively, in frequency of occurrence (Table 3.3). The crested goby was third in density (14.9% of all fishes), and ranked second in frequency of occurrence. Nine species were represented by one individual only (Table 3.3). The 10 most common fish species accounted for 89.8% of all fishes and had frequencies of occurrence ranging from 59.1 to 8.4%.

Fish species differences between habitat types were substantial. Thirteen species were present in only bay samples, and seven species were present in only beach samples (Table 3.3). In total, 16 species were collected in beach samples, 22 species occurred in bay samples, and nine species were common to both habitat types.

Table 3.3. List of nekton species in order of rank abundance, collected in exposed and protected seagrass habitat types in Bahia La Graciosa, Guatemala by drop sampling (12-18 June, 1994), with the total number of each species collected, the percentage of the total (908 specimens) caught, the number of samples in which the species was observed, and the percent frequency of the samples in which the species was observed (71 samples total). Species that were present in only one habitat type are indicated by (E) exposed or (P) protected.

Common Name	Scientific Name	Total number caught	Percent of total numbers	Number of samples present	Percent frequency of occurrence
Spotfin mojarra	*Eucinostomus argenteus*	129	14.21	42	59.15
Banded snapping shrimp	*Alpheus armillatus*	108	11.89	24	33.80
Southern pink shrimp	*Farfantepenaeus notialis*	102	11.23	34	47.89
Juvenile mojarra	*Eucinostomus* spp.	75	8.26	14	19.72
Crested goby (P)	*Lophogobius cyprinoides*	67	7.38	23	32.39
Hardhead silverside	*Atherinomorus stipes*	55	6.06	5	7.04
Dana swimming crab	*Callinectes danae*	36	3.96	19	26.76
Night shrimp	*Ambidexter symmetricus*	26	2.86	8	11.27
Banded blenny	*Paraclinus fasciatus*	24	2.64	13	18.31
American grass shrimp	*Periclimenes americanus*	23	2.53	11	15.49
Speck-claw decorator crab	*Microphrys bicornutus*	22	2.42	12	16.90
Knot-finger mud crab	*Panopeus lacustris*	18	1.98	12	16.90
Rock shrimp	*Sicyonia laevigata*	18	1.98	9	12.68
Truncate rubble crab	*Glytoplax smithii*	15	1.65	6	8.45

(table continued)

Urn crab	*Pitho quatridentata*	15	1.65	6	8.45
Squat grass shrimp	*Thor dobkini*	14	1.54	2	2.82
Shortchin stargazer (E)	*Dactyloscopus poeyi*	13	1.43	8	11.27
Arrow shrimp	*Tozeuma caroliniense*	13	1.43	6	8.45
Lined sole	*Achirus lineatus*	12	1.32	4	5.63
Sea bream (P)	*Archosargus rhomboidalis*	12	1.32	9	12.68
Emerald parrotfish (E)	*Nicholsina usta*	10	1.10	4	5.63
Marsh grass shrimp	*Palaemonetes vulgaris*	10	1.10	7	9.86
Green porcelain crab (E)	*Petrolisthes armatus*	10	1.10	4	5.63
Silver jenny	*Eucinostomus gula*	8	0.88	6	8.45
Goldline blenny (E)	*Malacoctenus aurolineatus*	7	0.77	6	8.45
Ground croaker (P)	*Bairdiella ronchus*	6	0.66	5	7.04
Central American toadfish	*Batrachoides gilberti*	5	0.55	5	7.04
Roughneck shrimp (E)	*Rimapenaeus constrictus*	5	0.55	3	4.23
Crested pipefish (E)	*Cosmocampus brachycephalus*	4	0.44	2	2.82
Slippery dick (E)	*Halichoeres vivittatus*	4	0.44	3	4.23
NCN* (P)	*Cyrtoplax spinidentata*	4	0.44	2	2.82
NCN* (E)	*Notolapas brasiliense*	4	0.44	2	2.82
Strongtooth mud crab	*Panopeus bermudensis* complex	4	0.44	4	5.63

(table continued)

Caribbean tonguefish	*Symphurus caribbeanus*	3	0.33	2	2.82
Common halfbeack (P)	*Hyporhamphus unifasciatus*	2	0.22	1	1.41
Juvenile corvina (P)	Sciaenid sp.1	2	0.22	1	1.41
Twin-spot bass (P)	*Serranus flaviventris*	2	0.22	2	2.82
Redfin needlefish	*Strongylura notata*	2	0.22	2	2.82
Stripped hermit crab (E)	*Clibanarius vittatus*	2	0.22	2	2.82
Lobate mud crab	*Euripanopeus abbreviatus* (nr.)	2	0.22	2	2.82
Furrowed mud crab	*Panopeus occidentalis*	2	0.22	2	2.82
Mayan cichlid (P)	*Cichlasoma urophthalmus*	1	0.11	1	1.41
Large-scaled spinycheek sleeper	*Eleotris ambliopsis*	1	0.11	1	1.41
Juvenile grunt (P)	*Haemulon* sp.	1	0.11	1	1.41
Hairy blenny	*Labrisomus nuchipinis*	1	0.11	1	1.41
Smooth trunkfish (P)	*Lactophrys triqueter*	1	0.11	1	1.41
Spaghetti eel (P)	*Moringua edwardsi*	1	0.11	1	1.41
Speckled worm eel (E)	*Myrophis punctatus*	1	0.11	1	1.41
Leatherjack (P)	*Oligoplites saurus*	1	0.11	1	1.41
Atlantic midshipman (P)	*Porichthys plectrodon*	1	0.11	1	1.41
Freshwater prawn (P)	*Macrobrachium acanthurus*	1	0.11	1	1.41
Cryptic teardrop crab (E)	*Pelia mutica*	1	0.11	1	1.41

(table continued)

Southern white shrimp (P)	*Litopenaeus schmitti*	1	0.11	1	1.41
Longfinger neck crab (E)	*Podochela riisei*	1	0.11	1	1.41

*NCN = No common name.

Thirty-two beach samples resulted in 130 fishes, dominated by spotfin mojarra, banded blenny, and shortchin stargazer in decreasing order of density (Table 3.4). Thirty-nine bay samples resulted in 288 fishes, dominated by spotfin mojarra, *Eucinostomus* sp.,crested goby, and hardhead silverside. In a test of density patterns for both the ten most common fishes and for total fishes across habitat types, Hotelling's T^2 revealed overall significant differences (T^2 value = 91.74, df = 70, $P < 0.0001$). Individual density differences for four species were found (LSMeans, df = 70, $P < 0.05$, with the BonFerroni correction), but the density of total fishes between habitat types was not significant (Table 3.4).

Mean number of fish species·m^{-2}, species richness (Margaleff's D), and sample evenness (Pielou's J) were similar in both habitat types (Table 3.4). Plots of fish cumulative diversity became asymptotic with roughly 15 samples for both habitat types, indicating a more than adequate characterization of these communities. Less than a 10% increase in cumulative diversity (H'_C) was observed with four samples for fishes collected in both habitat types (Fig. 3.3). Fish community diversity ($H'_{pop} \pm 95\%$ CI) in beach samples was estimated at 2.19 ± 0.05 and at 2.06 ± 0.08 in bay samples; however, overlapping CIs indicated non-significant differences between habitat types.

Using Spearman's Rank Correlation test, we were unable to reject the null hypothesis of no concordance between mean densities of the top ten fish species in beach and bay habitat types ($r = -0.2371$, $P > 0.5195$, $n = 10$). This is weak evidence that fish community structure was not similar, but was supported by ANOSIM results, (R value =

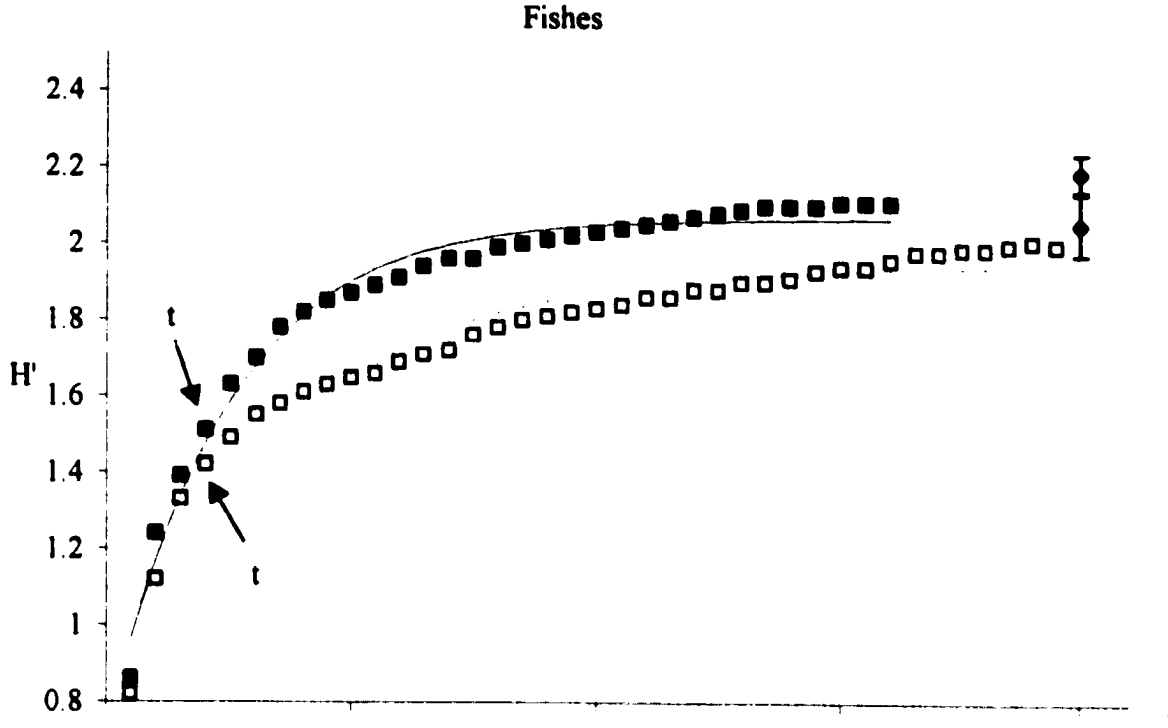
Table 3.4. Mean densities, individuals · m^2 (± 1 SE) for the most common (top ten species for each group) nekton species collected in exposed (beach) and protected (bay) seagrass habitat types in Bahia La Graciosa, Guatemala (12-18 June, 1994). Sample mean (± 1 SE) number of species·m^{-2}, diversity (Shannon-Wiener's H') species richness (Margaleff's D), and evenness (Pielou's J), are also listed. Each mean is estimated from 32 and 39 samples collected in beach and bay sites, respectively. Significant differences in means for total fishes, total crustaceans and individual species were detected (Hotelling's $T^2 = 151.41$, df = 70, $P < 0.0001$). In posterior testing, significant differences (LSMeans, df = 70, $P < 0.05$ corrected with the BonFerroni method) between bay and beach densities are indicated by different letters.

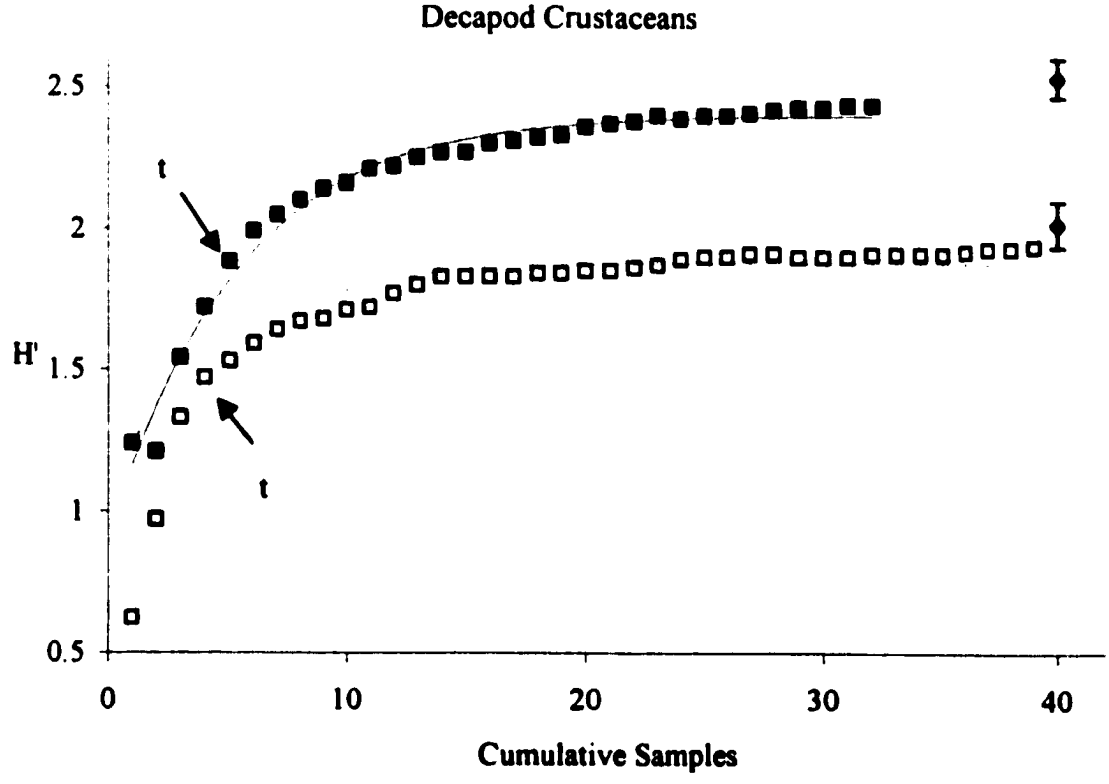
Species	Beach	Bay	Combined
FISHES (Total spp=29)			
Total fishes	3.37 ± 0.44 A	6.97 ± 1.36 A	5.35 ± 0.80
Spotfin mojarra	1.18 ± 0.39 A	1.81 ± 0.41 A	1.53 ± 0.29
Eucinostomus sp.	0.08 ± 0.06 A	1.55 ± 0.84 A	0.89 ± 0.47
Crested goby	0 ± 0 A	1.45 ± 0.28 B	0.79 ± 0.17
Hardhead silverside	0.24 ± 0.17 A	0.99 ± 0.97 A	0.65 ± 0.54
Banded blenny	0.58 ± 0.17 A	0.04 ± 0.03 B	0.28 ± 0.08
Shortchin stargazer	0.34 ± 0.12 A	0 ± 0 B	0.15 ± 0.06
Lined sole	0.05 ± 0.04 A	0.22 ± 0.19 A	0.14 ± 0.11
Sea bream	0 ± 0 A	0.26 ± 0.08 B	0.14 ± 0.05
Emerald parrotfish	0.26 ± 0.15 A	0 ± 0 A	0.12 ± 0.07
Silver jenny	0.11 ± 0.06 A	0.09 ± 0.05 A	0.09 ± 0.04
Number of species	1.82 ± 0.17	2.09 ± 0.16	1.97 ± 0.12
Sample diversity	0.64 ± 0.09	0.71 ± 0.06	0.68 ± 0.05
Sample richness	0.91 ± 0.13	0.89 ± 0.09	0.90 ± 0.07
Sample evenness	0.65 ± 0.08	0.69 ± 0.06	0.67 ± 0.05

(table continued)

CRUSTACEANS (Total spp=25)			
Total crustaceans	6.37 ± 1.29 A	4.64 ± 0.88 A	5.42 ± 0.76
Banded snapping shrimp	0.34 ± 0.17 A	2.05 ± 0.68 B	1.28 ± 0.39
Southern pink shrimp	1.79 ± 0.55 A	0.73 ± 0.19 A	1.21 ± 0.27
Dana swimming crab	0.76 ± 0.20 A	0.15 ± 0.06 B	0.43 ± 0.10
Night shrimp	0.66 ± 0.32 A	0.02 ± 0.02 A	0.31 ± 0.15
American grass shrimp	0.16 ± 0.11 A	0.37 ± 0.16 A	0.27 ± 0.10
Speck-claw decorator crab	0.53 ± 0.23 A	0.04 ± 0.03 B	0.26 ± 0.11
Knot-finger mud crab	0.03 ± 0.03 A	0.37 ± 0.11 B	0.21 ± 0.06
Rock shrimp	0.45 ± 0.17 A	0.02 ± 0.02 B	0.21 ± 0.08
Truncate rubble crab	0.03 ± 0.03 A	0.30 ± 0.15 A	0.18 ± 0.08
Urn crab	0.37 ± 0.24 A	0.02 ± 0.02 A	0.18 ± 0.11
Number of species	2.47 ± 0.34	1.88 ± 0.20	2.15 ± 0.19
Sample diversity	0.74 ± 0.12	0.60 ± 0.08	0.66 ± 0.07
Sample richness	0.93 ± 0.15	0.76 ± 0.10	0.84 ± 0.09
Sample evenness	0.53 ± 0.08	0.58 ± 0.07	0.56 ± 0.05

Figure 3.3. Sample and community diversity for fishes and decapod crustaceans for beach (■) and bay samples (□) collected in Bahia La Graciosa, Guatemala, in June 1994. Fitted lines represents an exponential increase in cumulative sample diversity on sample size for beach (solid line) and bay (dashed line) habitat types, with end points indicating the asymptotic cumulative sample diversity values (H'_A, see text). Letter t indicates the points at which cumulative diversity changed <10%. Community diversity values (H'_{pop}) ± 95% CI are represented for beach (◆) and bay (◇) sites.





0.342, $P < 0.00005$), and thus we rejected the null hypothesis of similar fish community structure between habitat types.

Fish Species Plots in Environmental Factor Space

In a plot of weighted mean factor scores for the ten most common fishes (Fig. 3.3), groups of species with different degrees of overlap were identified. First, shortchin stargazer, emerald parrotfish and banded blenny were located in intermediate seagrass coverage (Factor 1) in beach habitat type (Factor 2). Banded blenny separated from the other two species by selecting warmer and higher DO sites (Factor 3). Seabream and crested goby were located in high seagrass coverage in the bay habitat type. Hardhead silverside and spotfin mojarra were located in intermediate seagrass coverage in both beach and bay habitat types, but they separated along the temperature-DO gradient, where silverside selected higher levels. *Eucinostomus* sp. and lined sole located in bay habitat type in intermediate-low seagrass coverage. Finally, well separated from the other species, silver jenny were located in low seagrass coverage with intermediate values of sand sediment content, water temperature, and dissolved oxygen.

Decapod Crustacean Fauna

A total of 457 crustacean specimens were collected, including 25 species in 12 families (Table 3.3). The most important families were Majidae, represented by five species, Xanthidae represented by four species, Penaeidae and Palaemonidae represented by three species, and Goneplacidae and Hippolitidae represented by two species. Six other families were represented by one species only. The most abundant crustacean species, banded snapping shrimp, accounted for 23.6% of the total crustacean numbers,

followed by southern pink shrimp at 22.3% of the total crustacean abundance (Table 3.3). These species were second and first, respectively, in frequency of occurrence among the crustaceans. Third in density was the Dana swimming crab with 7.9% of the total crustaceans; followed by night shrimp at 5.7% of total crustaceans. Dana swimming crab was third in frequency of occurrence but night shrimp ranked eighth. The 10 most common species accounted for 83.8 % of all decapod crustaceans and had frequencies of occurrence that ranged from 47.9 to 8.4 %.

As with the fishes, crustacean species differences between habitat types were frequent. Six species were present only in beach samples and three species were present only in bay samples (Table 3.3). In total 22 species were collected in beach samples, nineteen species occurred in bay samples and sixteen species were common to both habitat types.

Beach samples resulted in 242 crustaceans, dominated by southern pink shrimp, Dana swimming crab, night shrimp, and speck-claw decorator crab in decreasing order of density (Table 3.4). Bay samples resulted in 215 specimens and were dominated by banded snapping shrimp, followed by southern pink shrimp, American grass shrimp, and knot-finger mud crab in decreasing order of density. In a test of density patterns for both the ten most common crustaceans and for total crustaceans across habitat types, Hotelling's T^2 revealed overall significant differences (T^2 value = 54.80, df = 70, $P < 0.0001$). In *a posteriori* tests, individual differences in densities for five species were found (LSMeans, df = 70, $P < 0.05$, with the BonFerroni correction), but total crustacean density was not significantly different (Table 3.4).

Mean number of species·m^{-2}, species richness (Margaleff's D), and evenness (Pielou's J) were similar for beach and bay habitat types (Table 3.4). Plots of cumulative diversity for the crustacean community (Fig. 3.3) approached an asymptote with approximately 10 samples, indicating a more than adequate characterization of the fauna in each habitat type. An increase of less than 10% in cumulative diversity was observed after five and four samples in beach and bay habitat types, respectively. Crustacean community diversity ($H'_{pop} \pm 95\%$ CI) was 2.54 ± 0.07 and 2.02 ± 0.08 on beach and bay habitat types, respectively, and non-overlapping 95% CI indicated significant differences.

Results of the Spearman's Rank Correlation test failed to reject the null hypothesis of no concordance in crustacean community structure between beach and bay habitat types when considering the top ten crustacean species ($r = -0.24001$, $P > 0.5042$, $n = 10$). This is only a weak indication that community structure is not similar in both habitat types, but when tested with ANOSIM, decapod crustacean beach and bay communities were significantly different (R value = 0.209, $P < 0.0005$).

Decapod Crustacean Species Plots in Environmental Factor Space

The plot of the ten most common decapod species in three-dimensional environmental space indicated distinct patterns of use of environmental conditions. Four species, rock shrimp, urn crab, Dana swimming crab, and speckled-claw decorator crab were associated with intermediate-high seagrass coverage (Factor 1) in beach habitat type (Factor 2). Another group, consisting of rubble crab and snapping shrimp, occupied intermediate-low seagrass coverage in bay habitat type. The rest of the species used unique suites of environmental conditions as the 95% CI of their centroids did not overlap.

Two species selected intermediate-low seagrass coverage areas, night shrimp in beach habitat type, and southern pink shrimp in both beach and bay habitat types. Knot-finger mud crab and American grass shrimp selected bay habitat type, grass shrimp used intermediate-high seagrass coverage whereas mud crab used the highest seagrass coverage. Compared to fishes, crustaceans appeared to avoid bare substrate, both in beach and bay habitat types.

Multiple Regression Analysis

The multiple linear regression model used to predict faunal density as a function of environmental variables identified percent seagrass coverage, percent of seagrass coverage^2, and salinity^2 (partial r^2 = 0.0524, 0.0364, 0.1196, respectively, all values significant at $P<0.05$) as significant in predicting total fishes density (model adjusted-r^2 = 0.3054; $P<0.002$; Mallow's Cp = 2.5267). For total crustaceans, the model identified temperature, temperature^2, and percent coverage (partial r^2 = 0.0254, 0.0280, and 0.0187, respectively, all values significant at $P<0.05$) as significant in predicting total crustacean density (model adjusted-r^2 = 0.1224; $P<0.0204$; Mallow's Cp = -6.9679). As most of the variance was left unexplained in these models, we examined whether blocking by habitat type would improve predictive power. Although some minor improvements were observed in the new model's adjusted- r^2, the increase partial-r^2 of individual variables were trivial and the results are not reported further.

Diel Changes in Species Density and Community Structure

When comparing densities of the ten most common fishes and crustaceans together with total fishes and total crustaceans in beach and bay habitats between day and night

samples, MANOVA indicated significant diel-by-habitat type interactions ($F = 2.2737$; $df = 10, 58$; $P < 0.0222$ and $F = 2.7634$; $df = 10, 58$; $P < 0.0061$ for fishes and crustaceans, respectively). Due to the presence of significant interactions, we could only compare cell means, but not main factor effects. Among fishes, hardhead silverside was the only species that showed significant diel differences in density, with the density of night samples significantly higher than day in beach habitat (LS Means, $df = 58$, $P < 0.05$, with the BonFerroni correction). Among crustaceans night shrimp and southern pink shrimp densities were significantly higher at night than during the day in beach habitat ($P<0.0006$). Knot-finger mud crab density in the bay was significantly higher during the night. Differences in total fishes or total crustaceans were significantly different between day and night ($P>0.05$, with the BonFerroni correction).

Results of the two-way crossed ANOSIM test for fish species indicated no significant diel effect ($R = 0.123$, $P > 0.06$), but we found a significant effect of habitat type ($R = 0.376$, $P < 0.0002$) when all 29 fish species were used in the analysis ($n = 65$ in both factors). One-way ANOSIM (Table 3.5) results indicated significant differences only when comparing beach-day vs. bay-day samples ($R = 0.395$, $P < 0.005$) and beach-day vs. bay-night samples ($R = 0.325$, $P < 0.001$). Similar results were obtained when the species number was reduced to the top twenty, ten, or five species (98, 80, and 78% of all individuals, respectively). For decapod crustaceans, the two-way crossed ANOSIM test also indicated no significant diel effect ($R = -0.144$, $P > 0.98$), but a significant effect of habitat type ($R = 0.120$, $P < 0.002$) when all 25 species were considered ($n=62$ for both effects). A one-way ANOSIM (Table 3.5) indicated significant differences only when

Table 3.5. Summary of one-way analysis of similarities comparing fish (n=65) and decapod crustacean (n=62) communities between exposed (beach) and protected (bay) seagrass habitat types during day and at night time.

	Fishes		Crustaceans	
Groups Compared	R-value	P-value	R-value	P-value
Beach vs. bay, day samples	0.395	0.005	0.102	0.007
Beach vs. bay, night samples	0.129	0.071	0.391	0.002
Day vs. night, beach samples	0.019	0.394	-0.124	0.884
Day vs. night, bay samples	0.197	0.045	-0.154	0.941
Day-beach vs. night-beach	0.325	0.001	0.064	0.236
Day-bay vs. night-beach	0.288	0.012	0.038	0.324

comparing beach-day vs. bay-day samples ($R = 0.102$, $P < 0.007$) and beach-night vs. bay-night samples ($R = 0.391$, $P < 0.002$). Similar results were obtained when the number of species was reduced to the top twenty, ten, and five (98, 84, and 64% of all individuals, respectively).

Three fish species were collected exclusively at night, including two redfin needlefish (one in each habitat type), one spaghetti eel, and one Atlantic midshipman (both collected in bay samples). No decapod crustaceans were collected exclusively at night.

Discussion

Structures of fish and decapod crustacean communities differed between exposed and protected habitat types. Bay samples resulted in more fish species, but beach samples had more decapod crustacean species, suggesting richer fish fauna in the bay and a richer crustacean fauna in beach habitats. Seven fishes were present only in beach areas, whereas thirteen were only found in bay samples. Decapod crustaceans, in contrast, included three species found exclusively in the bay, but six species found only in beach samples. However, although decapod crustacean community diversity was significantly higher in beach samples, no differences were found between beach and bay fish community diversities. Among the ten most common fishes, densities of two species were significantly higher in bay samples and two other species were higher in beach samples. Among the top ten decapod crustaceans, however, densities of three species were significantly higher in beach samples and two species were higher in bay samples. Two tests comparing community structure coincided in indicating different fish and decapod crustacean community structures between habitat types. When comparing the ranks of the

fish species between beach and bay, we noted that except for spotfin mojarra, which was the most abundant species in both habitat types, the other top four species were different. Among the top four decapod crustaceans species, southern pink shrimp was the only species common in both habitat types.

The effects of seagrass coverage we observed in protected and exposed habitat types on faunal abundance were similar to other studies that assessed the effects of wave exposure on seagrass faunas. In general, protected areas tend to have a higher abundance of organisms. Low-energy continuous seagrass beds have significantly higher shrimp density than high-energy patchy beds in North Carolina, USA (Murphey and Fonseca, 1995). However, O'Gower and Wacasey (1967) found significantly higher numbers of macrobenthic epifaunal and infaunal species in exposed compared with protected turtle grass beds (11.8 vs. 9.98 species per 50 samples, respectively) in Biscayne Bay, Florida. One possible explanation for this discrepancy may be that infauna are benefitted by the elevated food supply brought by increased water motion. However, inspection of their crustacean species mean densities indicates that of the ten species co-occurring in both environments, three species had higher mean densities in protected and three other species had higher mean densities in exposed habitats, whereas the other two have exactly the same density (O'Gower and Wacasey, 1967). Heck (1977) found higher abundance of southern pink shrimp, furrowed mud crab, and snapping shrimp in locations with muddy substrates in Panama seagrasses. We found that only banded snapping shrimp were significantly more abundant in muddy areas. Heck (1977) also found lower total faunal abundance and benthic vegetation on one of his four study sites (site 3), characterized as

the most protected and receiving the least wave shock; however, he also reported significantly lower species number where wave shock is most severe (site 2) and the sediment consists of calcareous sand. Nevertheless, he concluded that the overall effect of wave shock is to prevent establishment of seagrasses, instead of directly affecting invertebrate species. Pihl (1986) sampled the mobile epibenthic fauna off the Swedish coast, and found density, biomass, and annual faunal production to be significantly higher in vegetated, semi-exposed areas than in low- cover, exposed ones. He concluded that vegetation coverage is the major factor affecting the quantity of the mobile epibenthic fauna in shallow areas, whereas exposure has a major effect on the structure of the sediments, which seems to be an important factor for the production in unvegetated areas (Pihl, 1986). Orth (1977) found that the effect of simulated waves on experimental eelgrass plots is to significantly reduce the number of infaunal species; however, the effect on the total number of individuals is not always significant. Increased numbers of infauna in simulated waves treatments are associated with removal of the top sediment layer that uncovers *Zostera* rhizomes, which benefits dominant polychaete species. Nevertheless, this type of effect is only observed in nature along the edges of seagrass beds.

Differences in environmental variables between beach and bay sample sites in Guatemala helped to characterize these habitat types. The depth profile of the beach habitat type was characterized by its more moderate slope, which resulted in a shallower mean sample depths and allowed collection of samples at distances from shore that were ten times those sampled in the bay. Inside the bay, in contrast, depth profiles were much steeper, reducing the distance from shore that we could effectively use the drop sampler.

Exposure to wave action was the main factor responsible for differences observed between beach and bay habitat types. The beach was characterized by significantly higher sand substrate content, current velocity, and dissolved oxygen concentration, all factors related to wave energy. In contrast, bay samples had muddier substrates, lower current velocities, lower dissolved oxygen concentrations, and higher turbidities. Sediment composition can be an indirect measure of energy regime, with coarse, sandy sediments indicative of higher energy and fine sediments with high organic content indicative of lower energy (Fonseca et al., 1983). Similar to our results, Murphey and Fonseca (1995) and Irlandi (1996) reported significantly higher percent sediment fines and organic matter content in areas with low energy. Irlandi (1996) found no effect of energy regime on seagrass shoot density and blade length. Contrary to Irlandi's (1996) results, habitat type differences in our study were reflected in structural habitat characteristics of seagrass. Bay seagrass meadows had a significantly higher leaf area index and leaf biomass than beach meadows (2.2 and 1.6 times higher, respectively), both indicators of a higher seagrass density. This pattern might be related to a more nutrient rich environment, though we did not measure nutrient content; however, further sampling (Arrivillaga, unpublished data) found higher organic content levels in sediments from bay samples. Similarly, Pihl (1986) found a negative correlation between sediment organic content and exposure index. Our rotated factor analysis also identifyed seagrass and habitat type variables as responsible for explaining almost half of the environmental variation.

Seagrasses can significantly reduce wave energy and enhance sediment stability (Fonseca and Cahalan, 1992) by baffling currents and damping wave action (Orth, 1977).

Seagrass coverage decreases wave height and physical stress at the sediment-water interface. Suspended sediment concentrations are lower within seagrass beds compared to unvegetated sand and sedimentation rates are also significantly higher in seagrasses. Percent silt-clay and organic matter content of the surface sediments are negatively associated with shear velocity, suggesting that seagrass meadows in high energy areas are sources whereas meadows in low current areas are sinks of autochthonous detritus (Fonseca et al., 1983). Moreover, sediment particle size decreases and organic matter content increases going from the edge toward the center of seagrass beds (Orth, 1977). Our study also found these relationships, as bay samples were characterized by denser seagrass and lower sand sediment content. Bay sample sites were protected from wave energy by the surrounding mangrove forest, whereas beach sites were not only exposed to longer fetch but had also less densely structured seagrass meadows.

Faunal species groupings responded to the most important environmental variables, seagrass density and habitat type characteristics. Fish species centroids in three-dimensional environmental factor space (Fig. 3.3), indicated the use of unique sets of resources, although some overlap occurred. For decapod crustacean species much more overlap was observed, particularly along the habitat type axis (Factor 2). Also noteworthy was the absence of crustacean species at low levels of seagrass coverage, compared with fishes (Factor 1).

Overall variation in day/night faunal community structure was not significant; however, densities of one fish and three decapod crustacean species showed significantly higher night densities. No new decapod crustacean species were found uniquely in night

samples, but three uncommon fish species were only collected at night, evidence of the importance of night sampling in studies of biodiversity of seagrass meadows. Differences in total fish and crustacean densities from day to night in both habitat types were not significant. This result concurs with research in Australian seagrasses (Gray et al., 1998), where habitat-related differences in fish assemblages are stronger than diel changes, and seagrass assemblages remain similar day and night. Although the diversity and abundance of seagrass fishes are usually reported to be greater at night, a major reason may be that cryptic species are more susceptible to capture at night. Trawling is the most common method for collecting seagrass fishes, consequently day-time catches are a subset of the assemblage that is more vulnerable to being caught at night (Bell and Pollard, 1989). In the present study, the absence of significant differences between day and night densities of total fishes and total crustaceans densities was indicative of the efficiency of drop sampling, combined with rotenone, in characterizing the seagrass fauna, including cryptic species.

Studies of the diel effect on seagrass decapod crustaceans indicate similar species composition between day and night for caridean and penaeoid shrimp, but significantly higher mean night densities (Bauer, 1985a and b). In contrast to our results, Heck (1977) found the number of invertebrates to be significantly higher at night than during day time in Panama's seagrass beds. Although several species were collected exclusively at night and some species numbers were increased at night, no significance test was reported. These discrepancies may be related to differences in gear efficiency, as the otter trawl used in Panama is not highly efficient in seagrasses (Heck, 1977). Nocturnal species,

particularly carideans, become more susceptible to capture if they swim actively in the water column at night. We found resemblances between our results and those reported by Greening and Livingston (1982), reported no significant differences between diurnal and nocturnal species richness or numerical abundance, and a high level of similarity between day and night epibenthic macroinvertebrates in seagrasses. At the species level, Greening and Livingston (1982) found a few species to be significantly more abundant during the day or night, but the majority of species show no differences. Similar to our results, some species were found only in nocturnal samples and others were taken exclusively during the day in epibenthic crab scrape collections (Greening and Livingston, 1982). Night shrimp *Ambidexter symmetricus* and two species of pink shrimp were more abundant at night both in the present study (southern pink shrimp *Farfantepenaeus notialis*) and in Apalachee Bay, Florida (pink shrimp *F. duorarum*) (Greening and Livingston, 1982). Diel horizontal movements of fishes to and from seagrass beds have been documented and seem to be related to either foraging patterns (Robblee and Zieman, 1984) or tidal stage (Sogard et al., 1989). Diurnally inactive fishes move onto grass beds to feed at night from nearby coral reefs (Robblee and Zieman,1984), whereas Sogard et al. (1989) found diel movements of fishes on seagrass-covered banks in Florida Bay to be a response to tidal stage.

The majority of the specimens collected in this study were juveniles, and many are of economic importance in the region, including spotfin mojarra, seabream, silver jenny, ground croaker, Dana swimming crab, rock shrimp, southern white shrimp, and pink shrimp. The nursery function of seagrasses in the beach sector of the study area has been

demonstrated (Arrivillaga and Baltz, 1999), and in the present study we are able to prove this role for nearby seagrass meadows in protected environments like Bahia La Graciosa.

Although differences were found in community structure between beach and bay habitat types, overall species composition was representative of tropical seagrass areas. Studies on the Caribbean coast of Panama, Colombia, and Puerto Rico (Heck, 1977; Bauer, 1985a and b; Puentes and Campos, 1992) reveal that the most common shrimp species associated with turtle grass meadows are American grass shrimp, rock shrimp, and arrow shrimp, species also commonly found in the present study.

In summary, our study provided meaningful information on some of the important factors regulating fish and decapod crustacean communities in shallow tropical seagrass meadows. First, differences were found in seagrass fish and decapod crustacean community structures between sites exposed to different wave energy levels. Second, protected habitat types were richer in the number of fish species whereas exposed habitat types were richer in decapod crustacean species. Third, total fish and total crustacean densities were similar between protected and exposed habitat types, but density of some individual species were an order of magnitude greater in one habitat type. Fourth, differences were substantial for environmental variables between protected and exposed habitat types (depth profile, distance from shore, wave exposure, water velocity, sand sediment content, and seagrass structure). Finally, day-night patterns of fish and crustacean community structure were comparable, although significant diel effects were detected for the density patterns of a four species. This is the first study of the effects of

wave exposure on tropical seagrass fish and crustacean communities that relates seagrass characteristics to species composition and community structure.

Summary

Utilization of seagrass meadows by fishes and decapod crustaceans was described for exposed (beach) and protected (bay) estuarine habitat types near the mouth and inside of Bahia La Graciosa, Guatemala. The shallow bay has extensive turtle grass *Thalassia testudinum* meadows over muddy substrates. Around the bay mouth, a more exposed shoreline with sandy substrates also supports seagrass meadows. Using a cylindrical drop sampler, we quantitatively sampled the fauna at varying levels of seagrass coverage (0 to 100%). Physico-chemical variables and seagrass structural characteristics were also recorded for 71 samples, 32 in beach and 39 in bay, collected between June 12-18, 1994. Beach samples yielded 128 fishes of 16 species, dominated by spotfin mojarra *Eucinostomus argenteus*, banded blenny *Paraclinus fasciatus*, shortchin stargazer *Dactyloscopus poeyi*, and emerald parrotfish *Nicholsina usta*. Bay samples yielded 323 fishes of 22 species dominated by spotfin mojarra, juvenile mojarra *Eucinostomus* spp., crested goby *Lophogobius cyprinoides*, and hardhead silverside *Atherinomorus stipes*. Total fish densities between beach and bay sites were similar (mean ± 1S.E. = 3.37 ± 1.36 and 6.97 ± 0.44 fishes·m^{-2}, respectively), although densities of four fishes differed between habitat types ($P < 0.05$). Beach samples yielded 242 decapod crustaceans of 22 species, dominated by southern pink shrimp *Farfantepenaeus notialis*, Dana swimming crab *Callinectes danae*, night shrimp *Ambidexter symmetricus*, and speck-claw decorator crab *Microphrys bicornutus*. Bay samples yielded 215 crustaceans of 19 species dominated by

banded snapping shrimp *Alpheus armillatus*, southern pink shrimp, American grass shrimp *Periclimenes americanus*, and knot-finger mud crab *Panopeus lacustris*. Total crustaceans densities were similar between beach and bay sites (6.37 ± 1.29 and 4.64 ± 0.88 crustaceans·m^{-2}, respectively), although densities of five crustacean species differed ($P < 0.05$) between habitat types. An analysis of similarities of fish and crustacean species densities indicated significant (ANOSIM, $P < 0.0001$) differences in community structures between habitat types. Fish and decapod crustacean densities were related to eleven environmental variables in a factor analysis that explained 80% of the variance in five factors: a seagrass coverage axis, a substrate-distance-turbidity-depth axis, a temperature-dissolved oxygen axis, a current velocity axis, and a salinity axis. In factor space, the ten most abundant fishes and crustaceans each used unique combinations of environmental variables. No significant diel variations in community structure were detected when comparing sixteen night samples with day samples in a two-way crossed ANOSIM of fish and crustacean species ($P>0.06$). A MANOVA test of the ten most common fish and crustacean species indicated significant diel-by-habitat type interactions ($P<0.022$).

References

Arrivillaga, A. and D.M. Baltz. 1999. Comparison of fishes and macroinvertebrates on seagrass and bare-sand sites on Guatemala's Atlantic coast. Bull. Mar. Sci. 65, 301-319.

Bauer, R.T, 1985a. Diel and seasonal variation in species composition and abundance of caridean shrimps (Crustacea: Decapoda) from seagrass meadows on the North coast of Puerto Rico. Bull. Mar. Sci. 36, 150-162.

Bauer, R.T, 1985b. Penaeoid shrimp fauna from tropical seagrass meadows: species composition, diurnal, and seasonal variation in abundance. Proc. Biol. Soc. Wash. 98, 177-190.

Bell, J.D. and D.A. Pollard. 1989. Ecology of fish assemblages and fisheries associated with seagrasses. In: Larkum, A.W.D., MacComb, A.J., Shepherd, S.A., (Eds.), Biology of seagrasses. Aquatic Plant Studies 2. Elsevier, Amsterdam, pp. 565-609.

Blaber, S.J.M., D.T. Brewer, J.P. Salini, J.D. Kerr, and C. Conacher. 1992. Species composition and biomasses of fishes in tropical seagrasses at Groote Eylandt, Northern Australia. Estuar. Coast. Shelf Sci. 35, 605-620.

Buchanan, J.B., 1984. Sediment analysis. In: Holme, N.A., McIntyre, A.D. (Eds.), Methods for the study of marine benthos, Ch 3. Blackwell Scientific Publications. Oxford, pp. 41-65.

Carr, M.R., 1997. PRIMER user manual. Plymouth Marine Laboratory. Plymouth UK.

Clark, B.M., 1997. Variations in surf-zone fish community structure across a wave-exposure gradient. Estuar. Coast. Shelf. Sci. 44, 659-674.

Clarke, K.R. and R.H. Green. 1988. Statistical design and analysis for a 'biological effects' study. Mar. Ecol. Prog. Ser. 46, 213-226.

Clarke, K.R, 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117-143.

Clarke, K.R. and R.M. Warwick. 1994. Changes in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, UK, 144 pp.

Connolly, R.M., 1994. A comparison of fish assemblages from seagrass and unvegetated areas of a Southern Australian estuary. Aust. J. Mar. Freshwater Res. 45, 1033-44.

Duffy, K.C. and D.M. Baltz. 1998. Comparison of fish assemblages associated with native and exotic submerged macrophytes in the Lake Pontchartrain estuary, USA. J. Exp. Mar. Biol. Ecol. 223, 199-221.

Fisher, W. (Ed.), 1978. FAO species identification sheets for fishery purposes. Western Central Atlantic (fishing area 31). Vols. 1-7.

Fonseca, M.S., J.C. Zieman, G.W. Thayer, and J.S. Fisher. 1983. The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. Estuar. Coast. Shelf Sci. 17, 367-380.

Fonseca, M.S. and J.A., Cahalan. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. Estuar. Coast. Shelf Sci. 35, 565-576.

Fonseca, M.S. and S.S. Bell. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. Mar. Ecol. Prog. Ser. 171, 109-121.

Gee, G.W. and J.W. Bauder. 1982. Particle-size analysis. In: A. Klute (ed.) Methods of soil analysis. Part 1. Ch. 15. American Society of Agronomy, Inc. Soil Science Society of America, Inc. Publisher. Madison, pp. 383-411.

Gray, C.A., R.C. Chick, and D.J. McElligott. 1998. Diel changes in assemblages of fishes associated with shallow seagrass and bare sand. Estuar. Coast. Shelf. Sci. 46, 849-859.

Greening, H.S. and R.L. Livingston. 1982. Diel variation in the structure of seagrass-associated epibenthic macroinvertebrate communities. Mar. Ecol. Prog. Ser. 7, 147-156.

Grossman, G.D., P.B. Moyle, and J.O. Whitaker Jr. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. Amer. Nat. 120, 423-454.

Grossman, G.D., D.M. Nickerson, and M.C. Freeman. 1991. Principal component analyses of assemblage structure data: utility of tests based on eigenvalues. Ecology 72, 341-347.

Heck, Jr. K.L. 1977. Comparative species richness, composition and abundance of invertebrates in Caribbean seagrass (*Thalassia testudinum*) meadows (Panama). Mar. Biol. 41, 335-348.

Heck, Jr. K.L. and R.J. Orth. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In: Kennedy, V. S. (Ed.), Estuarine perspectives. Academic Press, New York, Pp 449-464.

Herbold, B., 1984. Structure of an Indiana stream fish association: choosing an appropriate model. Amer. Nat. 124, 561-572.

Irlandi, E.A, 1996. The effects of seagrass patch size and energy regime on growth of a suspension-feeding bivalve. J. Mar. Res. 54, 161-185.

Johnson, R.A. and D.W. Wichern. 1992. Applied multivariate statistical analysis. Prentice Hall, New Jersey, 642 pp.

Littel, R.C., R.J. Freund, and P.C. Spector. 1991. SAS System for linear models. Third Edition, SAS Institute Inc., Cary, NC, 329 pp.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, 547 pp.

Murphey, P.L. and M.S. Fonseca. 1995. Role of high and low energy seagrass beds as nursery areas for *Penaeus duorarum* in North Carolina. Mar. Ecol. Prog. Ser. 121, 91-98.

Neter, J., W. Wasserman, and M.H. Hutner. 1990. Applied linear statistical models: regression, analysis of variance, and experimental designs. Third Edition, Irwin, Boston. 1181 pp.

Ogden, J.C, 1980. Faunal relationships in Caribbean seagrass beds. In: Phillips, R.C., McRoy, C.P. (Eds.), Handbook of seagrass biology: an ecosystem perspective. Garland STPM Press, New York, pp.173-198.

Ogden, J.C. and E.H.Gladfelter (Eds.). 1983. Coral reefs, seagrass beds and mangroves: their interaction in the coastal zones of the Caribbean. Unesco Reports in Marine Science, 23. Montevideo, Uruguay. 133 pp.

O'Gower, A.K., and J.W. Wacasey. 1967. Animal communities associated with *Thalassia*, *Diplanthera*, and sand beds in Biscayne Bay. I. Analysis of communities in relation to water movement. Bull. Mar. Sci. 17, 175-210.

Orth, R.J., 1977. The importance of sediment stability in seagrass communities. In: B.C. Coull (ed.) Ecology of Marine Benthos. University of South Carolina Press, Columbia, pp. 281-300.

Orth, R. J., 1992. A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. In: John, D.M., Hawkins, S.J., Price, J.H. (Eds.), Plant-Animal Interactions in Marine Benthos. The Systematics Association Special Volume No. 46. Clarendon Press, Oxford. Pp. 147-164.

Ott, J.A., 1990. Biomass. In: Phillips, R.C., McRoy, C.P. (Eds.), Seagrass Research Methods, Chapter 8, UNESCO, Paris, pp. 55-60.

Perkins-Visser, E., T.G. Wolcott, and D.L. Wolcott. 1996. Nursery role of seagrass beds: enhanced growth of juvenile blue crabs (*Callinectes sapidus* Rathbun). J. Exp. Mar. Biol. Ecol. 198, 155-173.

Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. J. Theoret. Biol. 13, 131-144.

Pihl, L., 1986. Exposure, vegetation and sediment as primary factors for mobile epibenthic faunal community structure and production in shallow marine soft bottom areas. Neth. J. Sea Res. 20, 75-83.

Pinckney, J.L. and F. Micheli. 1998. Microalgae on seagrass mimics: Does epiphyte community structure differ from live seagrass? J. Exp. Mar. Biol. Ecol. 221, 59-70.

Pollard, D.A., 1984. A review of ecological studies on seagrass-fish communities, with particular reference to recent studies in Australia. Aquat. Bot. 18, 3-42.

Puentes, L.G. and N.H. Campos. 1992. Los camarones (Crustacea: Decapoda: Natantia) asociados a praderas de *Thalassia testudinum* Banks ex Koning, en la region de Santa Marta, Caribe Colombiano. Caldasia 17, 121-132.

Robins, C.R., R.M. Bailey, C.E. Bond, J.R. Brooker, E.A. Lachner, R.N. Lea, and W.B. Scott. 1991. Common and scientific names of fishes rom the United States and Canada (5th ed). Amer. Fish. Soc. Spec. Publ. no. 20, 183 pp.

Robblee, M.B., and J.C. Zieman. 1984. Diel variation in the fish fauna of a tropical seagrass feeding ground. Bull. Mar. Sci. 34, 335-345.

SAS Institute, 1989. SAS language and procedures. SAS Institute, Inc., Cary, version 6.

SAS Institute, 1985. SAS user's guide: statistics. SAS Institute Inc., Cary, NC, version 5, 941 pp.

Schlotzhauer, S.D. and R.C. Littell. 1987. SAS System for elementary statistical analysis. SAS Institute Inc., Cary, NC, 416 pp.

Sheldrick, B.H. and C. Wang, C. 1993. Particle size distribution. In: M.R. Carter (Ed.) Soil sampling and methods of analysis. Ch. 47. Lewis Publishers, Boca Raton, pp. 499-511.

Sogard, S.M., G.V.N. Powell, and J.G. Holmquist. 1989. Utilization by fishes of shallow, seagrass-covered banks in Florida Bay: 2. Diel and tidal patterns. Envirom. Biol. Fish., 24, 81-92.

Sogard, S.M. snf K.W. Able. 1994. Diel variation in immigration of fishes and decapod crustaceans to artificial seagrass habitat. Estuaries 17, 622-630.

Weinstein, M. P. and H.A. Brooks. 1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: community composition and structure. Mar. Ecol. Prog. Ser. 12, 15-27.

Williams, A.B., L.G. Abele, D.L. Felder, H.H. Hobbs Jr., R.B. Manning, P.A. McLaughlin, and I. Perez Farfante. 1988. Common and scientific names of aquatic invertebrates from the United States and Canada: decapod crustaceans. Amer. Fish. Soc. Spec. Pub. no. 17, 77 pp.

Zieman, J. C., and R.T. Zieman. 1989. The ecology of the seagrass meadows of the west coast of Florida: a community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85, 155 pp.

CHAPTER 4

HABITAT AND SEASONAL EFFECTS ON NEKTON COMMUNITY STRUCTURE IN TROPICAL TURTLE GRASS MEADOWS

Introduction

Nekton abundance in seagrass has been related to both habitat structure and seasonality. Habitat structuring factors such as leaf height and density (Bell and Westoby, 1986), plant biomass (Heck and Crowder, 1991), patch size (Holt et al., 1983; Eggleston et al., 1999), and current velocity (Murphey and Fonseca, 1995) have also been identified as important regulators of nekton community in seagrasses. Seasonal factors related to species abundance and composition, including food availability, larval supply, and differential temporal availability of adjacent habitat types, also affect nekton distribution in seagrass areas (Orth and van Montfrans, 1987; Pollard, 1984; Rozas and Minello, 1998).

Habitat type characteristics and seasonality have both been identified as factors affecting nekton community structure in seagrass systems; however, their relative importance in tropical systems has not been evaluated. Within habitat types, differences in exposure to wave energy may result in differential patterns of nekton species composition and abundance and have been studied in both temperate (O'Gower and Wacasey, 1967; Orth, 1977; Fonseca et al., 1983; Phil 1986; Fonseca and Cahalan, 1992; Murphey and Fonseca, 1995; Irlandi 1996; Clark, 1997; Pinckney and Micheli, 1998; Fonseca and Bell, 1998; Turner, 1999), and tropical seagrass systems (Heck, 1977; Bauer, 1985a and b; Arrivillaga and Baltz, submitted). The importance of seasonality in tropical versus temperate seagrass fauna abundance has also been examined (Heck, 1979; Aliaume et al.

1993). Nevertheless, while temporal changes in community structure have been evaluated in fish (Burchmore et al., 1984; Gray et al., 1996) and invertebrates (Connolly, 1997) in temperate seagrass systems, formal tests of significance are seldom reported (Aliaume et al. 1993; Louis et al., 1995) in studies of seasonality in tropical seagrass communities. In temperate seagrass systems, fluctuations in invertebrate abundance and species richness appear to be consequences of predation and seasonality. Seasonal changes in seagrass structural complexity brought about by the variation in water temperature (Heck, 1979) can strongly influence nekton. The numbers of nekton species and individuals in temperate seagrass systems are higher during the warmer months, often due to the arrival, around summer, of new recruits (Orth and van Montfrans, 1987). Their departure for other habitats in late autumn or winter often coincides with the seasonal cycle of seagrass dieback (Young, 1981; Pollard, 1984). In the tropics, lower species abundances seem to coincide with periods of reduced salinity associated with rainfall, but fluctuations are smaller than those in temperate systems because predators are present year round (Heck, 1979; Winstein and Heck, 1979) and because the magnitude of seasonal environmental variation is less than in temperate systems (Odum, 1974). In tropical systems, seasonality is generally related to rainfall and observed faunal fluctuations are often associated with the cycle of wet and dry seasons (Bauer, 1985). A strong positive relationship between rainfall and subsequent offshore commercial catch of adult shrimp is observed in tropical Australian estuaries, where increased emigration of juveniles is significantly correlated with increasing rainfall (Vance et al., 1998). Similarly, shrimp postlarvae entering the estuary and juveniles in the estuary show strong seasonal variation with the highest

numbers occurring just before and during the wet season (Vance et al., 1996). In tropical seagrass systems, seasonal patterns of nekton species densities may be variable with significant seasonal fluctuations in invertebrate (Heck, 1977); however, seasonal differences in fish species densities at the same location are not detectably different (Weinstein and Heck, 1979). Temporal patterns may also be inconsistent between years at the same location, with fish abundance differing significantly in one year (Yanez-Arancibia et al., 1988 and 1993), but not in another (Vargas-Maldonado and Yanez-Arancibia, 1997).

The Atlantic coast of Guatemala, though only 200 km long, supports important commercial and artisanal fisheries (Arrivillaga and Baltz, 1999). In this area, seagrasses are important marine habitat for fishes and decapod crustaceans and support significantly higher juvenile fish and crustacean densities than adjacent bare substrate sites (Arrivillaga and Baltz, 1999). Seagrass meadows support highly diverse fish and macroinvertebrate communities around the world (Ogden, 1980; Heck and Orth, 1980; Orth, 1992), and are essential nursery areas for many fishes, shrimp, and crabs (Ogden and Gladfelter, 1983; Weinstein and Brooks, 1983; Pollard, 1984; Zieman and Zieman, 1989; Blabber et al., 1992; Connolly, 1994; Perkins-Visser et al., 1996). Although the importance of environmental factors, such as exposure to wave energy, in affecting seagrass characteristics and seagrass fauna of tropical environments have been studied (Heck, 1977; Arrivillaga and Baltz, submitted), the relative importance of seasonality as a factor controlling nekton community structure in protected and exposed tropical seagrass systems has not been studied.

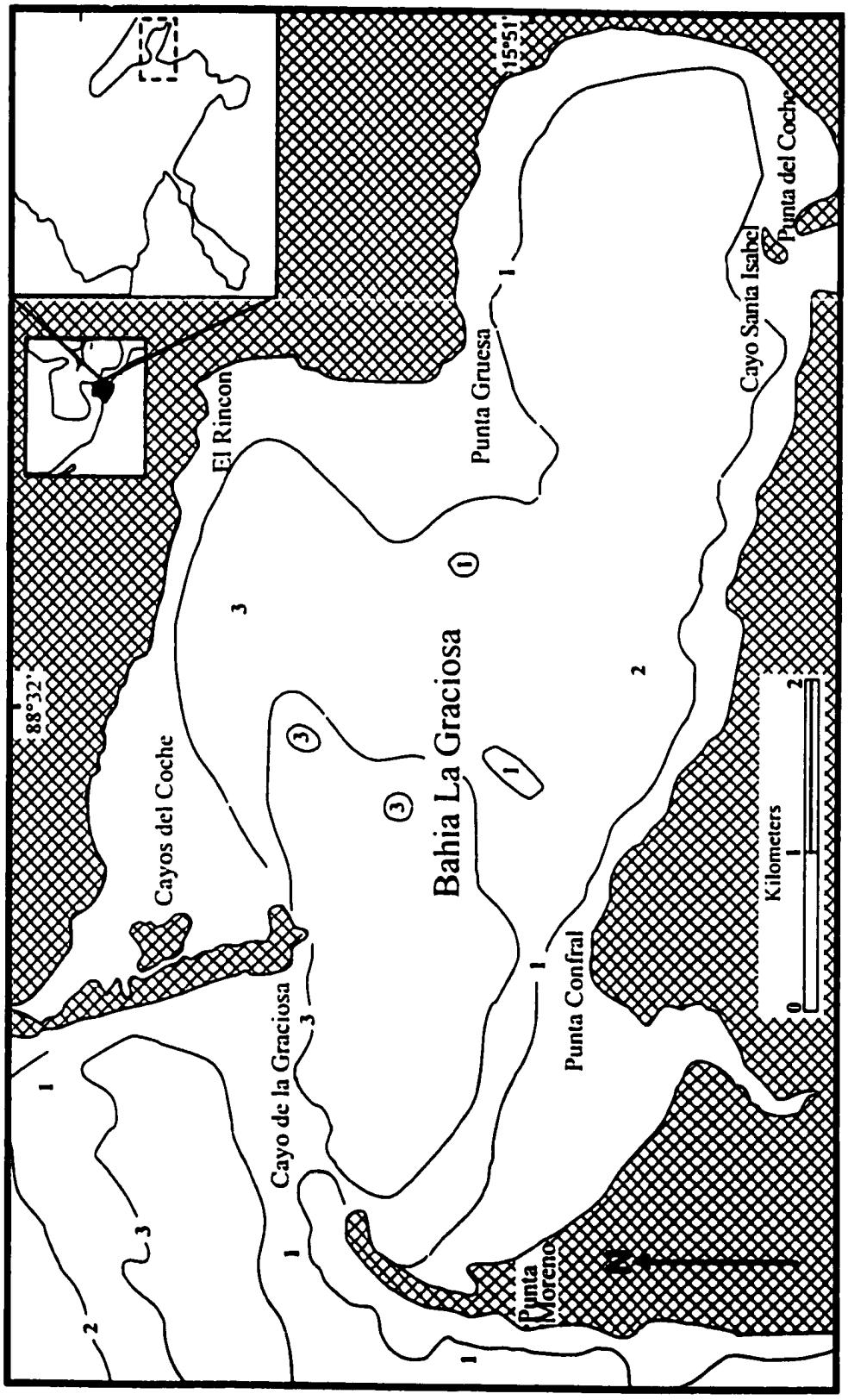
The objectives of this study were to evaluate seasonality (i.e., as reflected by rainy and dry periods) and variation in seagrass habitat types manifested by degrees of exposure to wave energy (i.e., protected and exposed) on the community structure of fishes and decapod crustaceans, and to compare environmental variables between seasons and habitat types. Our results showed that nekton community structure was affected primarily by habitat type and secondarily by seasonality and that interaction of both season and habitat type factors affected the densities of the some common species. The main environmental variables characterizing habitat type differences were seagrass leaf area and coverage, while current velocity and temperature were more strongly associated with seasonality.

Materials and Methods

Study Area

Bahia La Graciosa is a shallow bay, surrounded by red mangroves *Rhyzophora mangle*, located on Amatique Bay in the Gulf of Honduras, on the Caribbean coast of Guatemala (Fig. 4.1). It supports extensive seagrass beds consisting mainly of turtle grass (*Thalassia testudinum*). Sandy substrates dominate the bay's mouth and adjacent areas outside the bay, whereas most of the interior is dominated by clay-silt substrates. The mean depth inside the bay is 2.0 m and around the mouth it is 1.5 m. The shallow, high wave energy conditions typical of seagrass beds on sandy beaches around the bay's mouth differ substantially from more protected conditions in the muddy seagrass meadows inside the bay. The study area has a mesotidal pattern dominated by semi-diurnal tides with a maximum amplitude of 1 m. The climate is tropical and seasonal variation is limited (1980 to 1999 data from the Climatology Section of the Instituto Nacional de Sismologia,

Figure 4.1. Map of the study area, Bahia La Graciosa, Guatemala (depths in fathoms).



Vulcanologia, Meteorologia e Hidrologia -INSIVUMEH-, Guatemala, for Puerto Barrios Station, 15.74° N and 88.59° W). The primary freshwater influence in the region is from the Rio Dulce, located on the western side of Amatique Bay; however, direct precipitation into the Bahia La Graciosa drainage is also important. Rainfall occurs throughout the year (mean annual precipitation is 3.3 m) with a maximum monthly mean of 43.4 cm in August and a minimum monthly mean of 14.2 cm in March. A vaguely defined dry season occurs between January and May (monthly rainfall ranged between 14.2 and 26.2 cm) and a rainy season occurs between June and December (monthly rainfall ranged between 23.5 and 43.5 cm). The mean monthly air temperature in the area varies only slightly with a minimum of 23.5 °C in January and a maximum of 28.0 °C in July, while the yearly mean is 26.1 °C. Prevailing easterly winds tend to be stronger from October to April and lighter from May to September.

Sample Collection and Analysis

We used a drop sampler (Arrivillaga and Baltz, 1999) to conduct stratified random sampling of shallow exposed (beach) and protected (bay) seagrass habitat types during dry (14-17 December, 1993 and 6-11 January, 1995) and rainy (12-18 June, 1994) seasons. Gross sediment composition, quantitative observations of current velocity, and degree of exposure to wind-generated waves were used for initial stratification by habitat types. Five strata within each habitat type were identified and sampled equally. Individual sample sites within strata were selected randomly and considered to be statistically independent. The cylindrical drop sampler covered an area of 1.18 m^2 and consisted of a metal skirt and clear acrylic walls to reduce visual avoidance by nekton. The sampler was suspended from

a boom extending 2 m beyond the bow of a small (6 m) boat and about 0.4 m above the water's surface. A pull-pin release mechanism was used to drop the sampler on randomly selected sites in the range of depths suitable for the sampler (0 - 1 m). Upon deployment, and after firmly setting the sampler, a seawater solution of powdered rotenone (5% cube') was applied, and the fishes and decapod crustaceans swimming to the surface were collected with dip nets. We then swept the entire basal area thoroughly, with landing nets (Cummings Model 270-12", 5 mm mesh), to capture any remaining organisms until three successive passes yielded no additional individuals. This technique captures 96.5% of the nekton present in bare substrate and submerged aquatic vegetation sites (Duffy and Baltz, 1998). Small specimens were preserved directly in 95% ethanol, but larger organisms were preserved in a 10% buffered formalin solution, then transferred to 95% ethanol. Individuals were identified to species, counted, and measured to the nearest millimeter in standard length (SL) for fishes, carapace width (CW) for crabs, and carapace length (CL) for shrimp. Common names were assigned according to Fisher (1978), Williams et al. (1988), and Robins (1991).

Sampling was designed to collect a similar number of samples in beach and bay habitat types in both dry and rainy seasons, over the full range of seagrass bottom coverage (0 - 100 %), and to avoid major differences in environmental variables, especially depth and seagrass coverage. A total of 166 samples were collected, including 95 samples during the dry season (62 and 33 in beach and bay habitat types, respectively) and 71 samples during the rainy season (32 and 39 in beach and bay habitat types, respectively). At each sampling site, we recorded environmental variables, including minimum and

maximum depths, distance to the shore, substrate type (dominant and subdominant coding of sand, clay, and silt content), bottom visibility, turbidity in Nephelomenter Turbidity Units (NTU, Monitek, model 21 PE portable nephelometer), mid-water-column velocity (Montedoro-Whitney model PVM-2A portable velocity meter), water temperature (pocket thermometer), salinity (temperature-compensated refractometer, AO model 10419), dissolved oxygen concentration (YSI dissolved oxygen meter Model 57), percent of the bottom covered by seagrass, and shoreline vegetation. At each sampling site, a sediment core was collected. Later organic matter was oxidized with hydrogen peroxide and the remaining portion was analyzed for percent sand content by separating the sand and fine fractions and obtaining their respective dry weights (Buchanan, 1984; Gee and Bauder, 1986; Sheldrick and Wang, 1993).

Seagrass biomass and leaf characteristics at each sampling site were estimated by a 10 cm^2 core sample of the grasses to a substrate depth of 10 cm. Seagrass leaf biomass (g dry $wt \cdot m^{-2}$) was estimated as the weight of seagrass leaves (above-ground, green blades) after drying in a 60 °C oven to constant weight (Ott, 1990). We included any attached epiphytes and carbonate materials, but roots, rhizomes (short and long shoots), and drift algae were excluded (Sheridan, 1992). We also estimated a leaf surface area index (m^2 of leaf $area \cdot m^{-2}$ of substrate surface) from measurements of individual leaf length and width (above-ground, green blades) following Bulthuis (1990).

Statistical Analyses

Two MANOVA tests of a two-way crossed design (Littell et al., 1991; Johnson and Wichern, 1992) were used to evaluate the significance of seasons, habitat type, and

their interaction as factors influencing (1) environmental variables, and (2) densities (number·m^{-2}) for the 10 most common fish species and 10 most common decapod crustacean species and for total fishes and total crustaceans. For both environmental and faunal data sets, residuals of the initial MANOVA analyses (see below) were examined for normality using the Normal Procedure of SAS (Schlotzhauer and Littell, 1987). Where there was a lack of normality in the residuals, power transformations (x+1) (Johnson and Wichern, 1992) were used to achieve or approach normality before proceeding. When overall significant differences for main effects and/or interactions were detected with the MANOVA, Least Squares Means (LSMeans) posterior tests ($\alpha = 0.05$, with the BonFerroni correction) were performed to identify means that differed significantly (Littell et al., 1991).

A factor analysis of environmental data was used to describe the relationships among the eleven environmental variables and to reduce the number of environmental axes. Initial loadings were extracted by principal components using the correlation matrix. Varimax rotation (Proc Factor, SAS Institute, 1989) was used to generate a more readily interpretable structure (Johnson and Wichern, 1992). Factor scores for individual samples were plotted in three dimensions to examine their distribution in environmental space. Centroids representing means of all four habitat type and seasonal combinations were plotted as spheres with radii representing two standard errors (calculated as the mean standard error of the first three factors) around the mean to visualize differences between combinations. Similarly, sample factor scores were later used to explore species' locations in environmental space. Centroids of the first three factor scores (± 2 SE) were used to

identify the relative positions of species, along the first three major environmental gradients. For each species, factor scores were weighted using the density in each sample (Duffy and Baltz, 1998).

We examined cumulative diversity plots to determine if we had adequately characterized the fish and decapod crustacean groups with our sampling effort, to estimate the community diversity (H'_{pop}, sensu Pielou, 1966), and to compare community diversity between seasons and habitat types. Cumulative sample diversity was calculated in steps after sequentially pooling randomly selected samples until all samples were included. This procedure was repeated 50 times and means were obtained for each sample addition step. These means were fit to negative exponential functions using a non-linear regression procedure (SAS Institute Inc., 1985). Cumulative diversity step means together with their predicted values were plotted and visually examined to determine whether or not they approached an asymptote (Arrivillaga and Baltz, 1999). The point at which the asymptote was approached (t in Pielou, 1966) was identified as the number of cumulative samples that resulted in less than a 10% increase in cumulative diversity (Mueller-Dombois and Ellenberg,, 1974). Using this value, we estimated seasonal and habitat type community diversities (H'_{pop}) and their 95% confidence intervals (CIs) (Pielou, 1966), and judged comparisons to be significantly different when the CIs did not overlap.

We tested for significance of habitat and seasonal differences in community structure using an analysis of similarities (ANOSIM), applied to the similarity matrix of species-by-samples with the PRIMER statistical package (Carr, 1997). ANOSIM, is a Mantel type permutation combined with a general randomization approach to generate

significance levels (Monte Carlo tests). It is a non-parametric analog of a multivariate analysis of variance (MANOVA) (Clarke and Green, 1988; Clarke, 1993; Clarke and Warwick, 1994). Briefly, this method computes a test statistic reflecting the observed ranked similarities among samples in groups selected *a priori* (here habitat type and season combinations), and then contrasts this value with similarities among samples from randomly re-organized groups. The test statistic is R = (rW - rB) / (M/2), where M = n(n-1)/2. The total number of samples under consideration is n, rW is the mean of all rank similarities among samples within habitat type-season combinations and rB is the average of rank similarities from all pairs of samples between different habitat type-season combinations. Values of R will usually fall between zero and one, although they may range from -1 to +1. R is equal to one only if all samples of each habitat type-season combination are more similar to each other than they are to any samples from a different habitat type-season combination. R is approximately zero when the null hypothesis (H_0: 'no differences between seasons and habitat types') is true and similarities between and within habitat types are the same on average. Next, the statistic is re-computed under permutations of the sample identification labels, i.e. randomly assigning new identity to each sample. Under the null hypothesis there will be little effect on the mean value of R if the labels identifying which samples belong to which habitat type-season combination are arbitrarily re-arranged. This process is repeated a large number of times (T = 20,000 times in this study). Finally, the significance level is estimated by referring the original value of R to the frequency distribution of R's calculated by permutation of the sample identification. If H_0 is true, the likely spread of values of R is given by the random

rearrangement. When the true value of R was unlikely to have come from this distribution, we rejected the null hypothesis. Formally, if only a critical quantity (t) of the T simulated values of R are as large (or larger than) the observed R, then H_0 can be rejected at a significance level of 100 (t+1)/(T+1)%. For 20,000 simulations, t = 1000 is the critical value at $\alpha = 0.05$. Using this technique, we tested the null hypothesis of no significant differences in community composition among four seasons and habitat type combinations. Similarity matrixes, used to compute the R value in ANOSIM, were based on the Bray-Curtis similarity measure, and consisted of all samples containing fishes or decapod crustaceans (119 and 109 of 166 total samples were included in the fish and decapod crustacean analyses, respectively). Conservatively, only those species (15 fishes and 17 decapod crustaceans) whose abundances equaled or exceeded one percent of the total number of individuals were included in the analyses.

Results

Environmental conditions differed significantly between habitat types and seasons. In the overall MANOVA for environmental variables, significant main effects and interactions between the factors season and habitat type were detected ($F = 6.4203$, $df = 11, 148$; $P<0.0001$). In *a posteriori* testing (LSMeans, $P<0.05$ with the BonFerroni correction), interactions between main effects were significant for velocity, turbidity, temperature, salinity, and dissolved oxygen (Table 4.1). Most notably, current velocity was higher in dry season and temperature was higher in the rainy season. The effect of season on seagrass biomass was significant in both habitats, and the effect of habitat type

Table 4.1. Environmental data (Mean ± 1SE) for samples collected in rainy (12-18 June, 1993) and dry (14-17 December, 1993 and 6-11 January, 1995) seasons in exposed (beach) and protected (bay) seagrass habitat types in Bahia La Graciosa, Guatemala. Significant interaction between main effects were detected (MANOVA, $F = 6.42029$; $df = 11, 148$; $P<0.0001$). In posterior testing, significant differences (LSMeans, $df = 162$; $P<0.05$ with the BonFerroni correction) between cell means are indicated by different letters, reading horizontally.

	Dry season		Rainy season	
Variable	Beach	Bay	Beach	Bay
Depth (cm)	62 ± 2.5 A	78 ± 1.8 B	61 ± 3.2 A	73 ± 2.7 AB
Distance (m)	62 ± 9.8 A	7 ± 1.0 B	78 ± 12.2 A	7 ± 0.8 B
Current velocity ($cm \cdot seg^{-1}$)	2.6 ± 0.38 A	4.1 ± 0.49 B	0.04 ± 0.01 C	0.01 ± 0.01 C
Sediment sand content (%)	51.8 ± 5.41 A	69.7 ± 4.74 B	97.8 ± 0.25 A	79.3 ± 2.60 B
Turbidity	0.7 ± 0.12 A	0.4 ± 0.10 A	0.4 ± 0.07 A	1.7 ± 0.30 B
Temperature °C	25.9 ± 0.28 A	28.4 ± 0.27 B	30.8 ± 0.17 C	31.7 ± 0.18 C
Salinity (ppt)	22.1 ± 0.73 A	24.6 ± 0.72 A	27.3 ± 0.39 AB	27.2 ± 0.71 B
Dissolved oxygen ($mg \cdot l^{-1}$)	7.4 ± 0.12 A	7.3 ± 0.35 A	7.1 ± 0.22 AB	6.2 ± 0.26 B
Seagrass:				
Biomass ($g\ dw \cdot m^{-2}$)	21.6 ± 3.55 A	42.6 ± 5.87 AB	83.2 ± 14.18 BC	134.2 ± 18.19 C
Leaf area ($m^2 \cdot m^{-2}$)	0.7 ± 0.12 A	1.9 ± 0.25 BC	1.3 ± 0.21 AB	2.7 ± 0.36 C
Coverage (%)	51.8 ± 5.41 A	91.8 ± 4.64 B	59.2 ± 6.97 A	80.5 ± 5.75 B
N	62	33	32	39

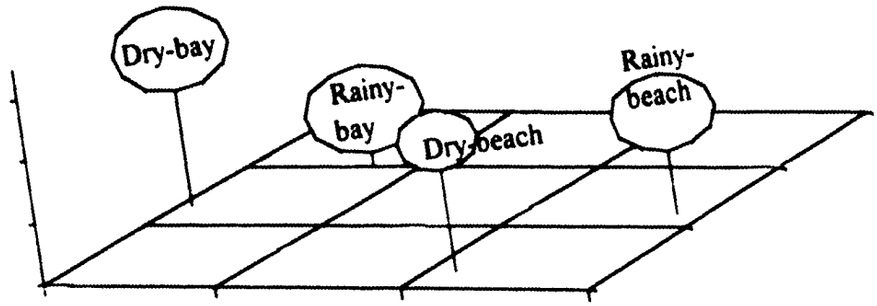
on depth, distance from shore, sediment percent sand content, seagrass leaf area index, and percent seagrass cover was significant on both seasons.

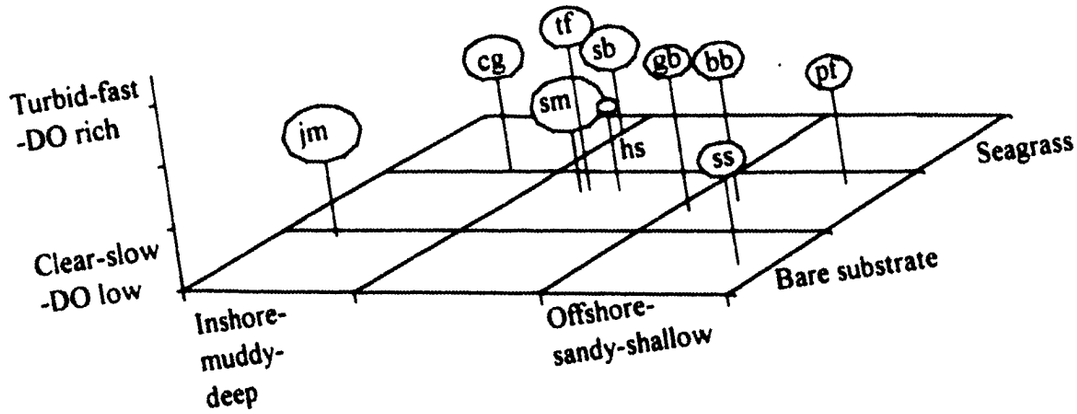
In the factor analysis, the first four factors had eigenvalues ≥ 1 and explained 71.1% of environmental variance (Table 4.2). Factor One loaded heavily for all seagrass variables (leaf area, leaf biomass, and percent of bottom covered by seagrass) and explained 23.2% of the total environmental variance. Factor Two loaded heavily for major habitat type differences (percent sand, distance from shore, and water depth) and explained 17.5% of the total variance. Factors three and four were identified as seasonality axes. Factor Three loaded heavily for turbidity, velocity, and dissolved oxygen concentration, explained 15.4% of total variance, and was identified as the primary season axis. Factor Four loaded heavily for salinity and temperature (15.0% of total variance) and was identified as the secondary season axis. The plot of centroids for season and habitat type combinations in three-dimensional-environmental space (Fig. 4.2a) revealed that most of the separation between habitat types occurred across Factor Two, while seasonal centroids separated along Factor Three, with dry season samples in both habitat types scoring higher than rainy season samples along this axis. Rainy season centroids for both habitat types scored higher on Factor One, seagrass abundance. Although bay samples tended to score higher than beach samples in Factor One for both seasons, samples from both habitat types encompassed the full range of seagrass coverage. Season and habitat type combination centroids and their confidence intervals indicated some overlapping of distributions along Factor One, but there was a clear separation of means along Factors Two and Three (Fig. 4.2a).

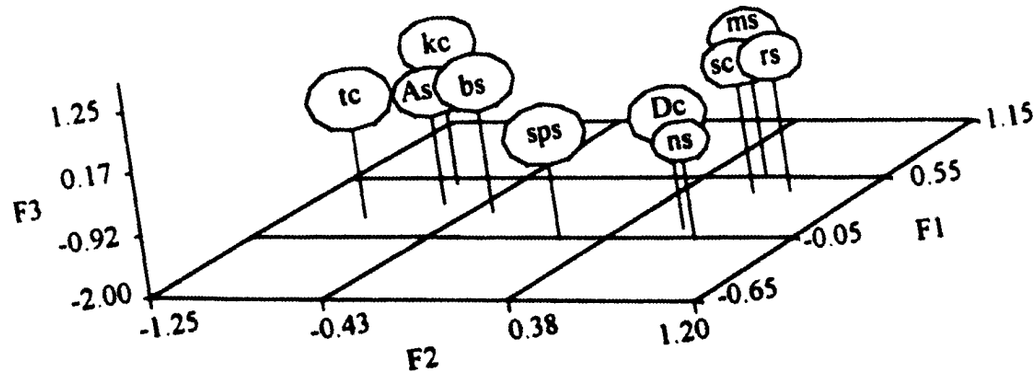
Table 4.2. Rotated factor loadings (VARIMAX rotation over five axes) for the environmental variables measured in 166 samples during dry and rainy seasons in exposed (beach) and protected (bay) seagrass habitat types in Bahia La Graciosa, Guatemala (14-17 December, 1993, 12-18 June, 1994, and 6-11 January, 1995). Numbers in boldface identify factors where variable scores are highest.

Variable	Factor 1	Factor 2	Factor 3	Factor 4
Leaf area	**0.9287**	-0.1810	-0.0453	0.1010
Leaf biomass	**0.9101**	-0.0181	-0.2245	0.2109
Percent seagrass cover	**0.6555**	-0.3968	0.3057	0.1161
Substrate % sand content	-0.3475	**0.7969**	0.0511	-0.1376
Distance	-0.2175	**0.7604**	0.0490	-0.0162
Depth	-0.3346	**-0.5134**	-0.0285	0.3437
Turbidity	-0.0294	0.1049	**0.8021**	0.1868
Velocity	-0.1142	-0.3017	**0.7768**	-0.1226
Dissolved Oxygen	0.0417	0.3472	**0.5315**	-0.0665
Salinity	0.0667	-0.0536	0.0910	**0.8862**
Temperature	0.3588	-0.1905	-0.0935	**0.7765**
Variance explained	2.5492	1.9292	1.6983	1.6482
% of total var. explained	23.17	17.54	15.43	14.98
% Cumulative var. explained	23.17	40.71	56.14	71.12

Figure 4.2. a) Season-habitat type combination centroids for dry and rainy seasons and beach and bay samples environmental data in three-dimensional factor space. The radii of balloons estimate two standard errors around the centroids. b) Fish and c) decapod crustacean species plot of centroids for the common ten species of each group in three-dimensional factor space. Species name abbreviations are: As=American grass shrimp; bb=banded blenny; bs=banded snapping shrimp; cg=crested goby; Dc=Dana swimming crab; gb=goldline blenny; hs=hardhead silverside; jm=juvenile mojarra; kc=knot-finger mud crab; ms=marsh grass shrimp; ns=night shrimp; pf=emerald parrotfish; rs=rock shrimp; sb=seabream; sc=speck-claw decorator crab; sm=spotfin mojarra; ss=shortchin stargazer; sps=southern pink shrimp; tc=truncate rubble crab; tf=Central American toadfish.







A total of 1751 specimens of 74 species was collected, including 44 fishes and 30 decapod crustacean species (Table 4.3). The ten most abundant nekton species accounted for 62% of all individuals and included (in order of abundance), banded snapping shrimp, spotfin mojarra, crested goby, southern pink shrimp, juvenile mojarra species, Dana swimming crab, hardhead silverside, knot-finger mud crab, banded bleny, and goldline bleny. The 20 most abundant nekton species accounted for 81.6% of the total number of individuals, whereas the 29 most abundant species accounted for 90.0% of the total number of individuals. Over half of the species (55%) were present in both seasons (41 species), whereas 18% (13 species) were only present in dry season samples and 27% (55 species) were only present in rainy season. Almost half of the species (46%) were present in both habitat types (34 species), whereas 32% (24 species) were only present in beach samples and 22% (16 species) were only present in bay samples. Twenty-nine species were present in only a particular season and habitat type combination, 18 of which were represented by single specimens.

The mean nekton species density (species$\cdot m^{-2}$), species richness (Margaleff's D), and sample evenness (Pielou's J) were similar between seasons for both habitat types (Table 4.4). Plots of cumulative diversity for fishes approached asymptotes, indicating that we had adequately characterized these communities (Fig. 4.3). We observed less than a 10% increase in cumulative diversity (H'_c) with between four and six samples for fishes collected in different season and habitat type combinations (Fig. 4.3). The mean for fish community diversity ($H'_{pop} \pm 95\%$ CI) during the dry season was estimated at 2.74 ± 0.09 and 1.92 ± 0.06 for beach and bay samples, respectively. For rainy season samples,

Table 4.3. List of nekton species in order of rank abundance, collected in rainy (12-18 June, 1993) and dry (14-17 December, 1993 and 6-11 January, 1995) seasons in exposed and protected seagrass habitat types in Bahia La Graciosa, Guatemala by drop sampling. Numbers are total number of each species collected, the percentage of the total (1751 specimens) caught, the number of samples in which the species was observed (166 total), and the percent frequency of occurrence. Species present in only one season and/or habitat type are indicated by (R) rainy, (D) dry, (E) exposed or (P) protected.

Common Name	Scientific Name	Total number caught	Percent of total numbers	Number of samples present	Percent frequency of occurrence
Banded snapping shrimp	*Alpheus armillatus*	269	15.36	47	28.31
Spotfin mojarra	*Eucinostomus argenteus*	156	8.91	54	32.53
Crested goby	*Lophogobius cyprinoides*	144	8.22	50	30.12
Southern pink shrimp	*Farfantepenaeus notialis*	137	7.82	56	33.73
Juvenile mojarra	*Eucinostomus* sp.	122	6.97	32	19.28
Dana swimming crab	*Callinectes danae*	67	3.83	40	24.10
Hardhead silverside (R)	*Atherinomorus stipes*	55	3.14	5	3.01
Knot-finger mud	*Panopeus lacustris*	54	3.08	32	19.28
Banded blenny	*Paraclinus fasciatus*	45	2.57	27	16.27
Goldline blenny (E)	*Malacoctenus*	43	2.46	20	12.05
Central American toadfish	*Batrachoides gilberti*	38	2.17	24	14.46
American grass	*Periclimenes americanus*	38	2.17	20	12.05
Marsh grass shrimp	*Palaemonetes vulgaris*	37	2.11	17	10.24
Green porcelain crab (E)	*Petrolisthes armatus*	36	2.06	11	6.63
Latin grunt (D-E)	*Haemulon steindachneri*	35	2.00	1	0.60
Truncate rubble crab	*Glyptoplax smithii*	33	1.88	20	12.05
Speck-claw	*Microphrys bicornutus*	33	1.88	20	12.05

(table continued)

Shortchin stargazer (E)	*Dactyloscopus poeyi*	29	1.66	17	10.24
Night shrimp	*Ambidexter symmetricus*	29	1.66	11	6.63
Rock shrimp	*Sicyonia laevigata*	29	1.66	15	9.04
Strongtooth mud crab	*Panopeus bermudensis* complex	23	1.31	12	7.23
Urn crab	*Pitho quatridentata*	20	1.14	8	4.82
Emerald parrotfish (E)	*Nicholsina usta*	18	1.03	10	6.02
Arrow shrimp	*Tozeuma caroliniense*	16	0.91	9	5.42
Sea bream (P)	*Archosargus rhomboidalis*	15	0.86	12	7.23
Crested pipefish (E)	*Cosmocampus brachycephalus*	15	0.86	9	5.42
Narrow back mud crab (D-E)	*Panopeus americanus*	15	0.86	7	4.22
Longtail grass shrimp (D-E)	*Periclimenes longicaudatus*	15	0.86	7	4.22
Furrowed mud crab	*Panopeus occidentalis*	14	0.80	6	3.61
Squat grass shrimp (R)	*Thor dobkini*	14	0.80	2	1.20
Lined sole	*Achirus lineatus*	13	0.74	5	3.01
Silver jenny	*Eucinostomus gula*	13	0.74	11	6.63
Ground croaker	*Bairdiella ronchus*	12	0.69	9	5.42
Roughneck shrimp (E)	*Rimapenaeus constrictus*	10	0.57	6	3.61
Twin-spot bass	*Serranus flaviventris*	8	0.46	8	4.82
Lobate mud crab	*Eurypanopeus*	7	0.40	6	3.61
Juvenile grunt	*Haemulon* sp.	6	0.34	3	1.81
Speckled worm eel	*Myrophis punctatus*	6	0.34	6	3.61

(table continued)

Mayan cichlid (P)	*Cichlasoma urophthalmus*	5	0.29	4	2.41
Slippery dick (E)	*Halichoeres vivittatus*	5	0.29	4	2.41
Juvenile corvina	Sciaenid sp1.	5	0.29	3	1.81
Caribbean tonguefish	*Symphurus caribbeanus*	5	0.29	4	2.41
Stripped hermit crab (E)	*Clibanarius vittatus*	5	0.29	5	3.01
Rainbow wrasse (D-E)	*Halichoeres pictus*	4	0.23	1	0.60
False pilchard (D-P)	*Harengula clupeola*	4	0.23	1	0.60
Burrowing mud crab (R-P)	*Cyrtoplax spinidentata*	4	0.23	2	1.20
NCN* (D-E)	*Hippolyte curacaoensis*	4	0.23	3	1.81
Horned spider crab (R-E)	*Notolapas brasiliense*	4	0.23	2	1.20
Shortfin pipefish (D-E)	*Cosmocampus elucens*	3	0.17	3	1.81
Common halfbeack (P)	*Hyporhamphus unifasciatus*	3	0.17	2	1.20
Cuban stone crab (D-E)	*Menippe nodifrons*	3	0.17	2	1.20
Large-scaled spinycheek sleeper	*Eleotris amblyopsis*	2	0.11	2	1.20
Darter goby (D-P)	*Gobionellus boleosoma*	2	0.11	1	0.60
Leatherjack	*Oligoplites saurus*	2	0.11	2	1.20
Redfin needlefish (R)	*Strongylura notata*	2	0.11	2	1.20
turtlegrass snapping shrimp (D)	*Synalpheus* sp.	2	0.11	2	1.20

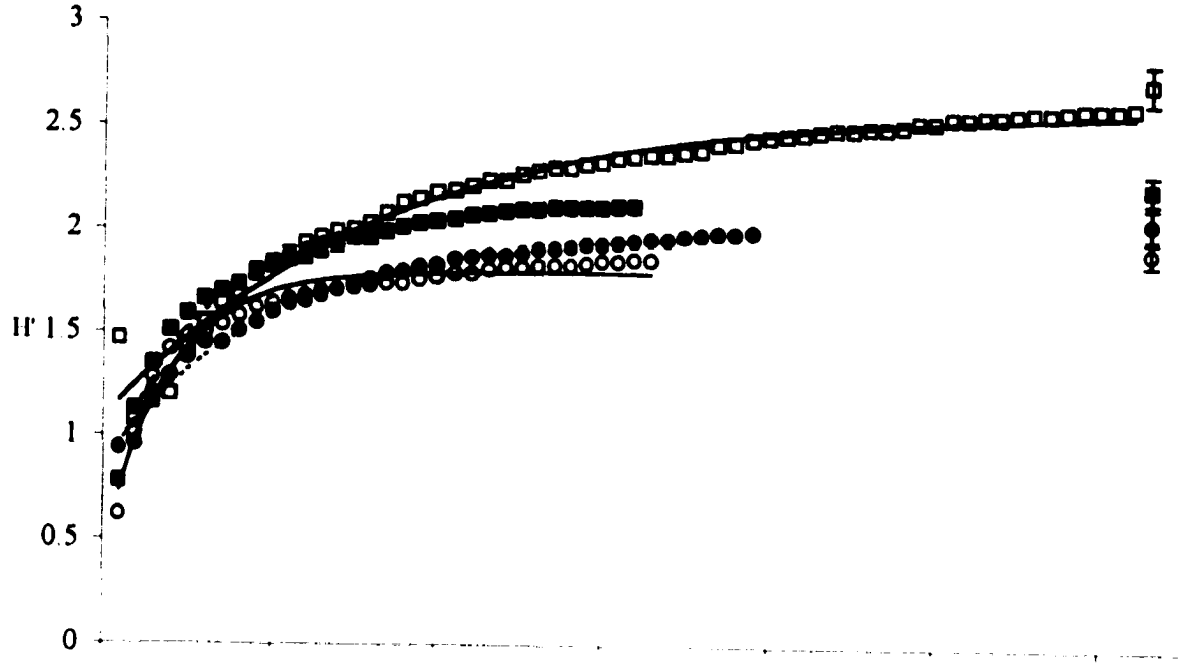
(table continued)

Stripped anchovy (D-P)	*Anchoa hepsetus*	1	0.06	1	0.60
Frillfin goby (D-E)	*Bathygobius soporator*	1	0.06	1	0.60
Emerald sleeper (D-P)	*Erotelis smaradgus*	1	0.06	1	0.60
Hairy blenny (R-E)	*Labrisomus nuchipinis*	1	0.06	1	0.60
Smooth trunkfish (R-P)	*Lactophrys triqueter*	1	0.06	1	0.60
Grey snapper (D-E)	*Lutjanus griseus*	1	0.06	1	0.60
Caribbean red snapper (D-E)	*Lutjanus purpureus*	1	0.06	1	0.60
NCN* (D-E)	*Malacoctenus delalandei*	1	0.06	1	0.60
Spaghetti eel (R-P)	*Moringua edwardsi*	1	0.06	1	0.60
Atlantic midshipman (R-P)	*Porichthys plectrodon*	1	0.06	1	0.60
Checkered puffer (D-P)	*Sphoeroides testudineus*	1	0.06	1	0.60
Great barracuda (D-P)	*Sphyraena barracuda*	1	0.06	1	0.60
NCN* (D-E)	*Symphurus tessellatus*	1	0.06	1	0.60
Dusky pipefish (D-P)	*Syngnathus floridae*	1	0.06	1	0.60
Freshwater prawn (R-P)	*Macrobrachium acanthurus*	1	0.06	1	0.60
Cryptic teardrop crab (R-E)	*Pelia mutica*	1	0.06	1	0.60
Southern white shrimp (R-P)	*Litopenaeus schmitti*	1	0.06	1	0.60
Longfinger neck crab (R-E)	*Podochela riisei*	1	0.06	1	0.60

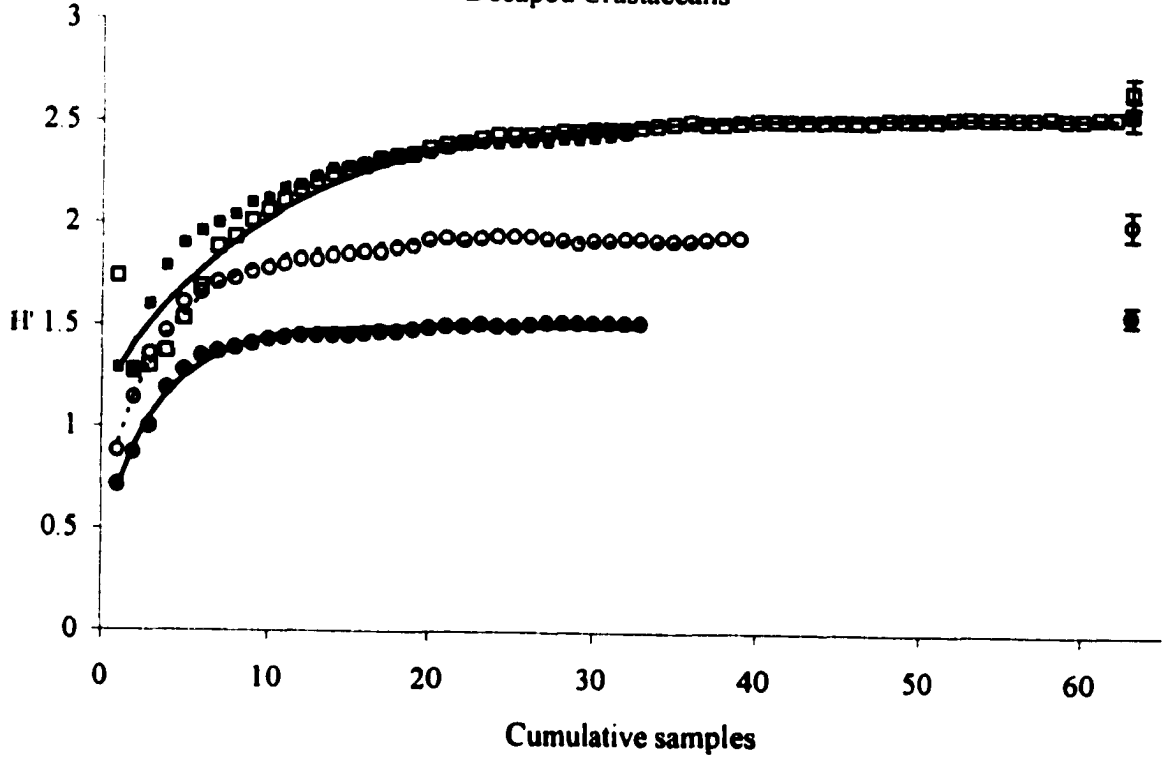
*NCN = no common name.

Figure 4.3. Sample and community diversity for fishes (a) and decapod crustaceans (b) for dry-beach (□), rainy-beach (■), dry-bay (○), and rainy-bay (●) samples collected in Bahia La Graciosa, Guatemala. Fitted lines represents an exponential increase in cumulative sample diversity on sample size for dry (solid line) and rainy (dashed line) seasons, with end points indicating the asymptotic cumulative sample diversity values (H'_A, see text). Letter t indicates the points at which cumulative diversity changed <10%. Community diversity values (H'_{pop}) ± 95% CI are represented for each season-habitat type combination.

Fishes



Decapod Crustaceans



cumulative diversity was estimated at 2.23 ± 0.07 and 2.06 ± 0.04 for beach and bay samples, respectively. Non-overlapping CIs indicated significant differences between all four of the season and habitat type combinations. In the case of crustacean decapods, cumulative diversity plots also approached asymptotes indicating that we had adequately characterized these communities. Less than a 10% increase in cumulative diversity (H'_C) was observed with between five and eight samples for crustaceans collected in the different season and habitat type combinations (Fig. 4.3). The mean for crustacean community diversity during the dry season was estimated at 2.68 ± 0.04 and 1.57 ± 0.05 for beach and bay samples, respectively. For rainy season samples, crustacean community diversity was estimated at 2.57 ± 0.07 and 2.02 ± 0.07 for beach and bay samples, respectively. Non-overlapping CIs indicated significant differences between seasons for bay samples, but we were unable to detect seasonal differences in beach samples.

In a two-way MANOVA test of density patterns for the 10 most common fish species and 10 most common decapod crustacean species and for total fishes and total crustaceans (Table 4.4), significant interactions were detected between season and habitat type effects (MANOVA F=1.8830, df =22, 141; P<0.0149). In *a posteriori* testing, significant differences in densities (LSMeans, df = 165, P < 0.05 with the BonFerroni correction) between habitat type-and-season combinations were detected for several species (Table 4.4). Comparison of LSMeans for densities indicated that three fish species, hardhead silverside, Central American toadfish, and emerald parrotfish, and two crustacean species, American grass shrimp and marsh shrimp, along with total crustaceans were not different across season or habitat type. A significant main effect for season was

Table 4.4. Mean (± 1 SE) densities (individuals · m^{-2}) for total fishes and total crustaceans and the most common (top ten species for each group) nekton species, number of species · m^{-2}, sample diversity, species richness, evenness, and the total number of species collected in exposed (beach) and protected (bay) seagrass habitat types in Bahia La Graciosa, Guatemala, in rainy (12-18 June, 1993) and dry (14-17 December, 1993 and 6-11 January, 1995) seasons samples. Combined densities are weighted means of densities from season-habitat type combinations. Significant interaction between habitat type and season effects was detected (MANOVA F=1.8830, df =22, 141; P<0.0149) for total fishes, total crustaceans and the density of the most common nekton species. In posterior testing, significant differences (LSMeans, df = 165, P < 0.05 with the BonFerroni correction) between cell means are indicated by different letters reading horizontally.

	Dry season		Rainy season		
Species	Beach	Bay	Beach	Bay	Combined
FISHES (Total = 44 spp)					
Total Fishes	2.8 ± 0.58 A	4.4 ± 0.52 B	3.4 ± 0.44 AB	7.0 ± 1.36 B	4.4 ± 0.46
Spotfin mojarra	0.2 ± 0.13 A	0.3 ± 0.11 A	1.2 ± 0.39 B	1.8 ± 0.41 B	0.9 ± 0.22
Crested goby	0.1 ± 0.05 A	1.8 ± 0.32 B	0 ± 0 A	1.4 ± 0.28 B	0.8 ± 0.23
Juvenile mojarra	0 ± 0 A	1.2 ± 0.31 C	0.1 ± 0.06 AB	1.5 ± 0.84 BC	0.7 ± 0.20
Hardhead silverside	0 ± 0	0 ± 0	0.2 ± 0.17	1.0 ± 0.97	0.3 ± 0.12
Banded blenny	0.3 ± 0.09 AB	0.03 ± 0.03 A	0.6 ± 0.17 B	0.04 ± 0.03 A	0.2 ± 0.06
Central American toadfish	0.3 ± 0.11	0.3 ± 0.09	0.03 ± 0.03	0.1 ± 0.04	0.2 ± 0.06
Goldline blenny	0.5 ± 0.15 A	0 ± 0 A	0.2 ± 0.07 A	0 ± 0 B	0.2 ± 0.03
Shortchin stargazer	0.2 ± 0.07 AB	0 ± 0 A	0.3 ± 0.12 B	0 ± 0 A	0.1 ± 0.06
Emerald parrotfish	0.1 ± 0.05	0 ± 0	0.3 ± 0.15	0 ± 0	0.1 ± 0.03

(table continued)

Sea bream	0 ± 0 A	0.1 ± 0.04 AB	0 ± 0 A	0.3 ± 0.08 B	0.1 ± 0.03
Number of species · m^{-2}	1.3 ± 0.18	2.1 ± 0.18	1.8 ± 0.18	2.1 ± 0.16	1.8 ± 0.09
Sample diversity	0.4 ± 0.07	0.7 ± 0.08	0.7 ± 0.10	0.7 ± 0.06	0.6 ± 0.04
Sample richness	0.5 ± 0.10	0.9 ± 0.12	0.9 ± 0.13	0.9 ± 0.09	0.8 ± 0.05
Sample evenness	0.3 ± 0.06	0.7 ± 0.07	0.6 ± 0.08	0.7 ± 0.06	0.6 ± 0.04
No. of species present	25	22	16	20	44
CRUSTACEAN (30 spp)					
Total crustaceans	4.3 ± 1.14	3.7 ± 0.82	6.4 ± 1.29	4.6 ± 0.88	4.8 ± 0.29
Banded snapping shrimp	1.2 ± 0.73 A	1.8 ± 0.64 AB	0.3 ± 0.17 AB	2.0 ± 0.68 B	1.4 ± 0.19
Southern pink shrimp	0.4 ± 0.09 A	0.2 ± 0.07 A	1.8 ± 0.55 B	0.7 ± 0.19 AB	0.8 ± 0.18
Dana swimming crab	0.4 ± 0.09 AB	0.03 ± 0.03 B	0.8 ± 0.20 A	0.1 ± 0.06 AB	0.3 ± 0.08
Knot-finger mud crab	0.1 ± 0.04 A	0.8 ± 0.21 B	0.03 ± 0.03 A	0.4 ± 0.11 AB	0.3 ± 0.09
American grass shrimp	0.1 ± 0.06	0.3 ± 0.11	0.2 ± 0.11	0.4 ± 0.16	0.2 ± 0.03
Truncate rubble crab	0.01 ± 0.01 A	0.4 ± 0.10 B	0.03 ± 0.03 A	0.3 ± 0.15 A	0.2 ± 0.05
Speck-claw decorator crab	0.1 ± 0.05 AB	0.03 ± 0.03 A	0.5 ± 0.23 B	0.04 ± 0.03 A	0.2 ± 0.06
Night shrimp	0.04 ± 0.02 A	0 ± 0 A	0.7 ± 0.32 B	0.02 ± 0.02 A	0.2 ± 0.08
Rock shrimp	0.1 ± 0.07 AB	0 ± 0 A	0.4 ± 0.17 B	0.02 ± 0.02 AB	0.2 ± 0.05
Marsh grass shrimp	0.3 ± 0.13	0.05 ± 0.04	0.2 ± 0.11	0.1 ± 0.04	0.2 ± 0.03
Number of species · m^{-2}	1.7 ± 0.25	1.7 ± 0.24	2.5 ± 0.34	1.9 ± 0.20	1.9 ± 0.09

(table continued)

Sample diversity	0.6 ± 0.08	0.5 ± 0.09	0.7 ± 0.12	0.6 ± 0.08	0.6 ± 0.02
Sample richness	0.7 ± 0.11	0.7 ± 0.13	0.9 ± 0.15	0.8 ± 0.10	0.8 ± 0.02
Sample evenness	0.4 ± 0.06	0.5 ± 0.08	0.5 ± 0.08	0.6 ± 0.07	0.5 ± 0.01
No. of species present	23	11	22	19	30
Number of samples	62	33	32	39	166

detected only for spotfin mojarra, with higher numbers during rainy season in both habitat types. A significant main effect for habitat type was detected only for crested goby, with higher numbers during rainy season in both habitat types. Significant interactions of main effects (Table 4.4) were detected for five fish species, five decapod crustacean species, and for total fish density. Habitat type effect was significant for juvenile mojarra, knot-finger mud crab, truncate rubble crab, and total fishes during dry season sampling, and for banded bleny, goldline bleny, shortchin stargazer, sea bream, speck-claw decorator crab densities during rainy season sampling. Densities of two other species, night shrimp and southern pink shrimp, showed a significant seasonal effect in beach samples only. Comparisons of banded snapping shrimp, Dana swimming crab, and rock shrimp densities were only significant between different habitat types and seasons.

Both season and habitat type effects were significant for fish community structure as tested with a two-way crossed ANOSIM, (R value = 0.152, and 0.407 for season and habitat type effects, respectively; $P<0.0002$ in both cases), and thus we rejected the null hypothesis of similar fish communities across seasons and habitats. For crustaceans, the habitat effect was significant (R value = 0.231; $P<0.0002$), but the seasonal effect was not (R value = 0.029; $P<0.098$). A one-way ANOSIM indicated significant differences in community structure between all four season and habitat type combinations for fishes ($P<0.0001$). A similar analysis failed to reject the null hypothesis for crustacean community structure between seasons for both habitat types ($P>0.239$ and $P>0.110$ for beach and bay samples, respectively), but detected differences in crustacean community structure between habitat types on both seasons ($P<0.001$). When comparing dry season

beach samples with rainy season bay samples, and when comparing dry season bay samples with rainy season beach samples, both fish and crustacean communities were significantly different in structure ($P<0.001$).

Mean factor scores for the ten most common fish species (Fig. 4.3c) were clearly dispersed along the first and second environmental axes. A group of three species, spotfin mojarra, hardhead silverside, and Central American toadfish, had strongly overlapping confidence intervals and were located in intermediate seagrass coverage in both seasons. Banded blenny and goldline blenny confidence intervals also overlapped in intermediate seagrass cover beach samples. Shortchin stargazer and juvenile mojarra confidence intervals were well separated from each other and from other species. Shortchin stargazer were associated with low seagrass cover beach samples, and juvenile mojarra were associated with low to intermediate seagrass cover bay samples. When we plotted the ten most common crustaceans in three dimensional environmental space (Fig. 4.3b), three species groups with different degrees of overlap were identified. In the first group, marsh grass shrimp, rock shrimp, and speckled claw decorator crab were located together in high seagrass coverage (Factor 1) in beach habitat samples (Factor 2). In the second group, banded snapping shrimp, American grass shrimp, knot-finger mud crab, and truncate rubble crab were associated in intermediate seagrass coverage bay samples. In the third group, night shrimp and Dana swimming crab with overlapping confidence intervals were closely associated in low seagrass coverage beach samples. The distribution of southern pink shrimp did not overlap with other species and was associated with low seagrass coverage in beach and bay habitats.

Discussion

Our results indicate that fish community structure in the study area was significantly affected by both habitat characteristics and seasonal variation, but decapod crustacean community structure was only affected by habitat characteristics. These observations were supported by analyses of similarities in community structure and concordance of species rank abundances (unpublished data). In general, the influence of habitat type appeared to have a stronger effect than season, particularly on crustaceans, in determining community structure. Differences in fauna between seasons and habitat types were basically expressed in terms of species composition, as total fish or total crustacean densities differed little among treatments. Moreover, in the analysis of individual densities of common species, the significance of habitat effects and season were not uniform, with several species showing no significant effects at all. In terms of individual species densities, the most common fish, spotfin mojarra, was the only species that showed a significant effect for season across habitats, and the second most abundant fish, crested goby, was the only species that showed a significant effect for habitat type across seasons. Interactions of season and habitat type factors were also important in determining individual species densities; however, habitat type affected densities of more individual species within a season than season did within habitats. Thus it appears that habitat type characteristics were comparatively more important than seasonality for the seagrass nekton communities reported in this study.

In tropical systems, seasonality is generally associated with rainfall and the cycle of rainy and dry seasons. In our study area, rainfall occurs throughout the year although an

oscillation in monthly rainfall is generally observed. The lowest rainfall occurs between February and May, whereas rainfall is highest between August and November. The beginning of the rainy season is around May-June, with a peak in August, and lasting through October or November. Rainfall is generally reduced for the rest of the year. Our first sampling trip in December 1993 coincided with the onset of the 1993-94 dry season. The second sampling trip in June 1994 occurred early in the rainy season. The third sampling trip in January 1995 fell at the onset of the 1995 dry season. Although total monthly rainfall in June 1994 was less than both December 1993 and January 1995, our rainy season collection was conducted after five months (January-May 1994) of reduced rainfall. We could consider 1994 as a slightly irregular year in that August and October monthly rainfall totals were extremely low; however, yearly precipitation in 1994 (3.2 $m \cdot year^{-1}$) was close to the 19-year rainfall average (3.3 $m \cdot year^{-1}$).

Because rainy season sampling was conducted during unusually dry conditions, it is appropriate to question whether or not our characterization of the turtle grass and its associated fauna was typical of a more normal rainy season. Seasonality in seagrass production and growth is controlled by the solar cycle and the associated cycle of temperature. In *Posidonia oceanica*, light and temperature are reported to account for 46.1% and 42.8% of the variability in shoot size and growth, respectively (Alcoverro et al., 1995). Light (Dennison, 1987; Perez-Llorens and Niell, 1993) and insolation (Jacobs, 1979) are the controlling factors in *Zostera marina* production. Biomass in *Zostera noltii* (Perez-Llorens and Niell, 1993), and photosynthesis in *Cymodocea nodosa* (Perez and Romero, 1992) show seasonal patterns with maxima in summer and minima in winter.

Tropical seagrass species like *Thalassia testudinum* also undergo seasonal fluctuation with maximum values of productivity and other biotic variables in the warmer summer months (Zieman, 1975). The response to seasonal forcing is species specific, as small seagrass species respond primarily to temperature fluctuations and large species respond primarily to seasonal light conditions. Large seagrass species such as *Thalassia* are also able to grow more independently of environmental conditions than small species due to photoassimilates storage and transport (Zieman, 1975; Marba et al., 1996). Although the rainfall pattern in the study area during 1994 was erratic, daylength followed a smooth annual cycle with a minimum of 11.3 hours in December and a maximum of 13.0 hours in June. The June sample occurred at maximum daylight photoperiod in which turtle grass would be expected to respond and did respond by having higher biomass which is a typical rainy season response. Thus we feel that our June sampling adequately described the turtle grass and fauna characteristics of the rainy season.

The importance of seasonality in seagrass nekton assemblages in both temperate and tropical systems is still equivocal. Tropical seagrass meadows contain larger numbers of nekton species, more rare species, and exhibit a more uniform distribution of relative abundances among species than comparable temperate communities (Heck, 1979). This greater uniformity is attributed to fewer environmental stresses and less seasonal variation in tropical seagrass biomass and leaf characteristics than in temperate seagrass communities (Odum, 1974). In contrast, temperate seagrasses experience pronounced seasonal temperature and salinity variations and also suffer marked declines of seagrass biomass during winter. Because temperate seagrasses are continually subjected to

disturbances that vary in space and time, the fauna may exist as a spatial and temporal mosaic of different species. Heck and Orth (1980) propose that both predator-prey relationships and the amplitude of seasonal fluctuations can be responsible for latitudinal differences in seagrass epibenthic invertebrate and juvenile fish populations. At high latitudes, periods of predator inactivity due to cold temperature allow invertebrates and juvenile fishes to escape predation and increase abundances early in the season. As predators grow and increase their feeding rates, prey population sizes drop dramatically resulting in cycles of large amplitude. Because populations of both invertebrates and fishes are present all year around in the tropics, standing crops and amplitudes of invertebrate population fluctuations are relatively low. Nevertheless, seasonal trends in abundance and species richness of invertebrates at both temperate and tropical areas are reported (Heck, 1979). Heck (1979) indicates that even though noticeable decreases in abundance occur in tropical areas that coincide with the height of the rainy season and lowered salinity, abundances in tropical Panama, are significantly lower and never show the large fluctuations that characterize temperate systems on Florida's Gulf coast. Another plausible explanation for the relatively high diversity of tropical versus temperate seagrass faunas may be derived from the intermediate disturbance hypothesis (Connell, 1978) that predicts that species diversity within habitats will be maximal at intermediate levels of disturbance (Diel and Roughgarden, 1998). In the tropics, disturbances due to seasonal changes in rainfall and temperature are not as strong as in temperate regions; however, seasonal disturbances are substantial and may combine with storms and other perturbations to maintain higher diversity in tropical coral reef systems (Aronson and

Precht, 1995). When comparing seasonality between temperate (Portugal) and tropical (Guadeloupe) seagrass fish species abundance, Aliaume et al. (1993) report that high spring and summer variability in Portugal is related to recruitment to the seagrass system, while reduced fall and winter variability is due to migration out of the system. In Guadeloupe seasonal variability is related to changes in sedentary species' abundances. Studies in Australia report contrasting results regarding the significance of seasonality as a factor controlling community structure for temperate seagrass faunas. Connolly (1997) reports significant differences among sampling periods when comparing epifaunal assemblage structure. Similarly, Gray et al. (1996) indicate consistent differences between two sampling periods in the assemblage structure of fishes associated with seagrass. In contrast, Burchmore et al. (1984) report significant correlation between spring and autumn fish samples.

Seasonal changes in dominant seagrass macrofauna species densities, associated with seasonal variation in water temperature, salinity, and seagrass biomass are reported in temperate locations. In Rookery Bay, Florida, Sheridan (1992), found that high fish abundances during spring and summer are associated with high temperature, salinity, and seagrass biomass. In Rookery Bay, as in Guatemalan seagrass meadows, spotfin mojarra, night shrimp, and pink shrimp show seasonal variation in density. Summer and autumn abundances of these species in Rookery Bay seagrasses are higher than in winter and spring. Snapping shrimp, also show seasonal variation in abundance in Rookery Bay seagrasses, but this species only showed seasonal changes in Guatemala when comparing between habitat types. In general, a shift in the order of dominance is observed with

changing seasons in Rookery Bay invertebrates. In Guatemala, in contrast, order of dominance for crustaceans was relatively stable across seasons but fish species rank abundances changed with season. Temporal variations in the settlement patterns of four sciaenid fishes occur in subtropical beds of *Halodule wrigthtii* in Port Aransas, Texas (Rooker, et al., 1998). The use of seagrass beds by these juvenile fishes is staggered over time with little overlap among the four most common species. Inshore spawners inhabit seagrasses during spring and summer while offshore spawners are present in late autumn and spring. In temperate seagrass systems (Francour, 1994), considerably reduced seasonal variation (indicated by low coefficients of variation) occurs in the fish fauna in a Mediterranean marine reserve when compared with areas outside the reserve, an effect that may be related to the protected status of the reserve stations. Rozas and Minello (1998) were able to demonstrate seasonal variations in the use of adjacent seagrass, saltmarsh, and nonvegetated habitat types in a south Texas estuary. Seasonal changes in brown shrimp habitat selection (Rozas and Minello, 1998) is related to variation in water depth between fall and spring. In autumn, when the water level is high, brown shrimp are distributed between the flooded marsh and seagrass, but in spring when marsh flooding is reduced, shrimp concentrate in seagrass. This change in habitat use is also related to high *Spartina* biomass in autumn and high seagrass biomass in spring. In contrast, in temperate Australia's *Posidonia australis* seagrasses, Ferrell et al. (1993) report that differences in the number of fish species and individual species abundances among estuaries separated by at least 100 km is not consistent at all times of the year. In three Australian estuaries (Ferrell et al., 1993), differences within estuaries are large and the interaction of time and

estuary are significant. In another Australian study, Young (1981) reports that summer species abundance and frequency of occurrence of subtropical epibenthic fauna in *Zostera capricorni* and *P. australis* are significantly greater than winter, and that species richness and composition varies with time with a minima in midwinter (June). Yearly variability is also significant in that some years winter abundances are as large as summer abundances in other years (Young, 1981).

The effect of seasonality on tropical seagrass faunal communities is not always as conclusive as in temperate areas. Significant seasonal fluctuations of invertebrate abundances occur in Panama's Caribbean tropical turtle grass beds (Heck, 1977). During the rainy season (April-November), salinity is low and drastic reductions may occur during heavy downpours. Declines, in both abundance and number of species in November and December, coincide with periods of large salinity decreases. Qualitative and quantitative changes in species composition also occur during those months (Heck, 1977). The southern pink shrimp in Panama meadows is one of the few species in which a seasonal pattern of abundance can be detected. We saw a similar pattern in Guatemala for this species. In Panama, decreases in shrimp abundance are associated with declining salinity (Heck, 1977). In January, with the increasing salinity accompanying the changeover from wet to dry season, species richness and abundance begin to increase and continue to rise through April. In contrast, in the same Panama collections, Weinstein and Heck (1979) were unable to detect significant seasonal differences in fish species composition and abundance. Neither fish species richness or abundance are related to salinity in Panama and no consistent pattern is apparent between protected and exposed locations (Weinstein

and Heck, 1979). The presence of juveniles of many species throughout the year may indicate a lack of distinct spawning seasons.

In Puerto Rico, another tropical location, seasonal effects are not spatially consistent for decapod crustacean abundance patterns in turtle grass (Bauer, 1985a and b). Shrimp fauna (Superfamily Penaeoidea) varied seasonally but only at one of Bauer's (1985a) two study locations. Significant seasonal changes in abundance of two rock shrimp, *Sicionia parri* and *S. laevigata*, are also inconsistent, although juvenile *Metapenaeopsis* show strong seasonal fluctuations (Bauer, 1985b). In contrast, the abundances of the principal caridean shrimp species show marked seasonal variation (Bauer, 1985a), even though variation in water temperature is not marked and no pronounced salinity variations exist. For Terminos Lagoon, Mexico, Yanez-Arancibia et al. (1993 and 1988) also report distinct seasonal patterns in tropical seagrass fish community biomass, density, number of species, and species dominance, where seasonality is related to precipitation, river discharge, and wind. A shift of the peak of fish biomass between the dominant habitat types, seagrasses, seagrass-mangroves, and fluvial-lagoon systems, is thought to be related to the time of maximum primary productivity in each habitat type. In contrast, an earlier study of seagrass fishes in Terminos Lagoon (Vargas-Maldonado and Yanez-Arancibia, 1987) found no significant seasonal effects in species abundance or diversity. In tropical Australian seagrasses, Vance et al. (1996) report strong seasonal variations in the catch of grooved tiger prawn, *Penaeus semisulcatus*, with highest numbers before and during the wet season. The most significant factor determining the abundance of juvenile tiger prawn in the estuary is the number of benthic

postlarvae that settles on the seagrass, while rainfall is the most important environmental variable in the postlarval catch (Vance et al., 1996). In Martinique (French West Indies), Louis et al. (1995) indicate significant differences among quarterly sampling periods for seagrass fish species richness and individual species densities; however, no significant effect of time on total abundance, biomass, diversity of evenness is apparent. Louis et al (1995) also observe that a tendency exists for a decrease in species richness during the dry season; however, overall numbers and biomass remain stable due to modifications of species abundances.

We observed that different species used different suites of environmental variables and that resource partitioning was common (Ross, 1986); however, overlap between some species was substantial. This is indicative of high habitat variability which in turn results in higher diversity and species richness. Although the total number of species collected was large, 70% of the species were uncommon and accounted for less than one percent total number of individuals. Nekton diversity was higher in beach samples than bay samples; however, the effect of season was not as clear. This leads us to infer that wave energy creates a more dynamic environment where more diverse habitat characteristics are maintained by a higher level of disturbance. The impact of wave generated disturbances appear to reduce the competitive dominance of some species, allowing for a greater diversity in terms of number of species to appear .

In conclusion, our results indicated that although both seasonal and habitat effects were significant in structuring tropical seagrass nekton communities, the effects of habitat type were stronger. Habitat type also had a primary effect on environmental variables and

season was secondary. Among the environmental variables studied, a seasonal effect was only detected on seagrass biomass. Seagrass biomass in turn was, together with seagrass leaf area index and coverage, primarily responsible for the environmental variability, while variables related to habitat type were of secondary importance. In our study on the Atlantic coast of Guatemala, where the dry season was poorly demarcated, seasonality was not as important as habitat type in structuring the communities of seagrass decapod crustaceans.

Caveat Lector

This is a first attempt to evaluate the relative importance of seasonality and habitat type on seagrass nekton community structure. Unfortunately, rainy season sampling in this study was conducted during an unusually dry month. Moreover, this was an unreplicated study and our data might underestimate the influence of seasonality. Thus, it may prove to be true that seasonality is equal to or even more important in some years when differences between dry and rainy seasons are more pronounced. Further research over a complete annual cycle and during multiple years should improve our understanding of the relative importance of seasons and habitat types on seagrasses and their fauna. For the present, this study indicated that seagrass habitat type significantly influenced community structure and that this effect was present during both dry and rainy season months. This information can guide the design of future experimental studies and provide researchers with a framework for the evaluation of other factors related to the ecology of seagrass fishes and macroinvertebrates.

Summary

We studied seagrass fish and decapod crustacean community structure in protected (bay) and exposed (beach) habitat types during rainy and dry seasons on the Atlantic coast of Guatemala. The study area, Bahia La Graciosa, is a shallow bay with extensive turtle grass *Thalassia testudinum* meadows over muddy substrates. Adjacent to the mouth, a more exposed shoreline also supports turtle grass meadows over sandy substrates. Seasonality is characterized by rainy (June - November) and dry (December - May) months, although rain occurs throughout the year. Using a cylindrical drop sampler, we quantitatively sampled the fauna at varying levels of seagrass coverage (0 to 100%) during both seasons. Physico-chemical variables and seagrass structural characteristics were also recorded for 166 samples, collected in two seasons and habitat types. Environmental conditions differed significantly inside and outside the bay and seasonally. A total of 1751 specimens of 74 species were collected, including 44 fish and 30 crustacean species. The ten most abundant nekton species accounted for 62% of all individuals and included (in order of abundance) banded snapping shrimp, *Alpheus armillatus*, spotfin mojarra, *Eucinostomus argenteus*, crested goby, *Lophogobius cyprinoides*, southern pink shrimp, *Farfantepenaeus notialis*, juvenile mojarra species, *Eucinostomus* spp., Dana swimming crab, *Callinectes danae*, hardhead silverside, *Atherinomorus stipes*, knot-finger mud crab, *Panopeus lacustris*, banded blenny, *Paraclinus fasciatus*, and goldline blenny, *Malacoctenus aurolineatus*. Over half of the species (55%) were present in both seasons and almost half of the species (46%) were present in both habitat types. Significant interactions were detected between season and habitat type effects for the density of the

ten most common fishes, and the ten most common decapod crustaceans, together with total fishes and total crustaceans. In *a posteriori* testing, significant differences between the densities of habitat type and season combinations were detected for several species. Separate analyses of similarities of fish and crustacean species densities indicated significant (ANOSIM, $P < 0.0002$) differences in community structures between habitat types, but the same analyses between seasons were significant only for fishes. Fish and decapod crustacean densities were related to eleven environmental variables in a factor analysis that explained 71.1% of the environmental variance in four factors: a seagrass coverage axis, a habitat type axis, and two seasonality axes. The structures of Guatemalan seagrass communities that we characterized were primarily affected by habitat type and secondarily by seasonality.

References

Alcoverro, T. C.M. Duarte, and J. Romero. 1995. Annual growth dynamics of *Posidonia oceanica*: contribution of large-scale versus local factors to seasonality. Mar. Ecol. Prog. Ser. 120: 203-210.

Aliaume, C., C. Monteiro, M. Louis, T.L. Hoai, and G. Lasserre. 1993. Spatial and temporal organization of lagoon fish communities (Ria Formosa in Portugal and Grand Cul de-Sac Marin in Guadeloupe). Oceanol Acta 16:291-301.

Aronson, R.B. and W.F. Precht. 1995. Landscape patterns of reef coral diversity: a test of the intermediate disturbance hypothesis. J. Exp. Mar. Biol. Ecol. 192: 1-14.

Arrivillaga, A. and D.M. Baltz. 1999. Comparison of fishes and macroinvertebrates on seagrass and bare-sand sites on Guatemala's Atlantic coast. Bull. Mar. Sci. 65, 301-319.

Arrivillaga, A. and D.M. Baltz. submitted. Fish and decapod crustacean community structure in exposed and protected seagrass environments on the Atlantic Coast of Guatemala.

Bauer, R.T. 1985a. Diel and seasonal variation in species composition and abundance of caridean shrimps (Crustacea: Decapoda) from seagrass meadows on the North coast of Puerto Rico. Bull. Mar. Sci. 36, 150-162.

Bauer, R.T. 1985b. Penaeoid shrimp fauna from tropical seagrass meadows: species composition, diurnal, and seasonal variation in abundance. Proc. Biol. Soc. Wash. 98, 177-190.

Bell, J.D. and M. Westoby. 1986. Importance of local changes in leaf heigh and density to fish and decapods associated with seagrasses. J Exp Mar Biol. Ecol. 104: 249-274.

Blaber, S.J.M., D.T. Brewer, J.P. Salini, J.D. Kerr and C. Conacher. 1992. Species composition and biomasses of fishes in tropical seagrasses at Groote Eylandt, Northern Australia. Est. Coast. Shelf Sci. 35: 605-620.

Buchanan, J.B. 1984. Sediment analysis. In: Holme, N.A., McIntyre, A.D. (Eds.), Methods for the study of marine benthos, Ch 3. Blackwell Scientific Publications. Oxford, pp. 41-65.

Bulthuis, D.A. 1990. Leaf surface area. Pages 69-70 *in* R. C. Phillips and C. P. McRoy, eds., Seagrass Research Methods, Chapter 11, UNESCO, Paris.

Burchmore, J.J., D.A. Pollard, and J.D. Bell. 1984. Community structure and trophic relationships of the fish fauna of an estuarine *Posidonia australis* seagrass habitat in Port Hacking, New South Wales. Bot. Mar. 18: 71-87.

Carr, M.R. 1997. PRIMER user manual. Plymouth Marine Laboratory. Plymouth UK.

Clark, B.M. 1997. Variations in surf-zone fish community structure across a wave-exposure gradient. Estuar. Coast. Shelf. Sci. 44, 659-674.

Clarke, K.R. and R.H. Green. 1988. Statistical design and analysis for a 'biological effects' study. Mar. Ecol. Prog. Ser. 46, 213-226.

Clarke, K.R 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117-143.

Clarke, K.R. and R.M. Warwick. 1994. Changes in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, UK, 144 pp.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.

Connolly, R.M. 1997. Differences in composition of small, motile invertebrate assemblages from seagrass and unvegetated habitats in a southern Australian estuary. Hydrobiologia 346: 137-148.

Connolly, R.M. 1994. A comparison of fish assemblages from seagrass and unvegetated areas of a Southern Australian estuary. Aust. J. Mar. Freshwater Res. 45: 1033-44.

Dennison, W.C. 1987. Effects of light on seagrass photosynthesis, growth, and depth distribution. Aquat. Bot. 27: 15-26.

Diel, R. and J. Roughgarden. 1998. Theory of marine communities: the intermediate disturbance hypothesis. Ecology 79: 1412-1424.

Duffy, K.C., and D.M. Baltz. 1998. Comparison of fish assemblages associated with native and exotic submerged macrophytes in the Lake Pontchartrain estuary, USA. J. Exp. Mar. Biol. Ecol. 223, 199-221.

Eggleston, D.B., W.E. Elis, L.L. Etherington, C.P. Dahlgren, and M.H. Posey. 1999. Organism responses to habitat fragmentation and diversity: habitat colonization by estuarine macrofauna. J. Exp. Mar. Biol. Ecol. 236:107-132.

Ferrell, D.J., S.E. McNeill, D.G. Worthington, and J.D. Bell. 1993. Temporal and spatial variation in the abundance of fish associated with the seagrass *Posidonia australis* in South-eastern Australia. Aust. J. Mar. Freshwater Res. 44: 881-899.

Fisher, W. (Ed.). 1978. FAO species identification sheets for fishery purposes. Western Central Atlantic (fishing area 31). Vols. 1-7.

Fonseca, M.S. and S.S. Bell. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. Mar. Ecol. Prog. Ser. 171, 109-121.

Fonseca, M.S., J.C. Zieman, G.W. Thayer, and J.S. Fisher. 1983. The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. Estuar. Coast. Shelf Sci. 17, 367-380.

Fonseca, M.S. and J.A. Cahalan. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. Estuar. Coast. Shelf Sci. 35, 565-576.

Francour, P. 1994. Pluriannual analysis of the reserve effect on ichthyofauna in the Scandola natural reserve (Corsica, Northwestern Mediterranean). Oceanol. Acta, 17: 309-317.

Gee, G.W. and J.W. Bauder. 1982. Particle-size analysis. In: A. Klute (ed.) Methods of soil analysis. Part 1. Ch. 15. American Society of Agronomy, Inc. Soil Science Society of America, Inc. Publisher. Madison, pp. 383-411.

Gray, C.A., D.J. McElligott, and R.C. Chick. 1996. Intra and inter estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. Mar. Freshwater Res. 47: 723-735.

Heck, Jr. K.L. 1977. Comparative species richness, composition and abundance of invertebrates in Caribbean seagrass (*Thalassia testudinum*) meadows (Panama). Mar. Biol. 41, 335-348.

Heck, K.L. Jr. 1979. Some determinants of the composition and abundance of motile macroinvertebrate species in tropical and temperate turtlegrass (*Thalassia testudinum*) meadows. J. Biogeogr. 6: 183-200.

Heck, K.L. Jr. and R.J. Orth. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In: Kennedy, V. S. (Ed.), Estuarine perspectives. Academic Press, New York, Pp 449-464.

Heck, K.L. Jr. and L.B. Crowder. 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. Ch. 14: 281-295 *in* S. S. Bell, E. D. McCoy and H. R. Mushinsky, eds. Habitat Structure: The physical arrangements of objects in space. Chapman and Hall, New York. 434 pp.

Holt, S.A., C.L. Kitting, and C.R. Arnold. 1983. Distribution of young red drums among different sea-grass meadows. Trans. Amer. Fish. Soc. 112: 267-271.

Irlandi, E.A 1996. The effects of seagrass patch size and energy regime on growth of a suspension-feeding bivalve. J. Mar. Res. 54, 161-185.

Jacobs, R.P.W.M. 1979. Distribution and aspects of the production and biomass of eelgrass, Zostera marina L. at Roscoff, France. Aquat. Bot. 7: 151-172.

Johnson, R.A. and D.W. Wichern. 1992. Applied multivariate statistical analysis. Prentice Hall, New Jersey, 642 pp.

Littel, R.C., R.J. Freund, and P.C. Spector. 1991. SAS System for linear models. Third Edition, SAS Institute Inc., Cary, NC, 329 pp.

Louis, M., C. Bouchon, and Y. Bouchon-Navaro. 1995. Spatial and temporal variations of mangrove fish assemblages in Martinique (French West Indies). Hydrobiologia 295: 275-284.

Marba, N., J. Cebrian, S. Enriquez, and C.M. Duarte. 1996. Growth patterns of Western Mediterranean seagrasses: species-specific responses to seasonal forcing. Mar. Ecol. Prog. Ser. 133: 203-215.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, 547 pp.

Murphey, P.L. and M.S. Fonseca. 1995. Role of high and low energy seagrass beds as nursery areas for *Penaeus duorarum* in North Carolina. Mar. Ecol. Prog. Ser. 121, 91-98.

Odum, H.T. 1974. Tropical marine meadows. In: H.T. Odum, B.J. Copeland, and E.A. McMahon (Eds.) Coastal Ecological Systems of the United States. Pp 442-487. Washington: The Conservation Foundation.

Ogden, J. C. 1980. Faunal relationships in Caribbean seagrass beds. In: Phillips, R.C., McRoy, C.P. (Eds.), Handbook of seagrass biology: an ecosystem perspective. Garland STPM Press, New York, pp.173-198.

Ogden, J.C. and E.H. Gladfelter (Eds.), 1983. Coral reefs, seagrass beds and mangroves: their interaction in the coastal zones of the Caribbean. Unesco Reports in Marine Science, 23. Montevideo, Uruguay. 133 pp.

O'Gower, A.K. and J.W. Wacasey. 1967. Animal communities associated with *Thalassia*, *Diplanthera*, and sand beds in Biscayne Bay. I. Analysis of communities in relation to water movement. Bull. Mar. Sci. 17, 175-210.

Orth, R. J. 1992. A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. In: John, D.M., Hawkins, S.J., Price, J.H. (Eds.), Plant-Animal Interactions in Marine Benthos. The Systematics Association Special Volume No. 46. Clarendon Press, Oxford. Pp. 147-164.

Orth, R.J. and J. van Montfrans. 1987. Utilization of a seagrass meadow and tidal marsh creek by blue crabs Callinectes sapidus. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. Mar. Ecol. Prog. Ser. 41: 283-294.

Orth, R.J. 1977. The importance of sediment stability in seagrass communities. In: B.C. Coull (ed.) Ecology of Marine Benthos. University of South Carolina Press, Columbia, pp. 281-300.

Ott, J.A. 1990. Biomass. In: Phillips, R.C., McRoy, C.P. (Eds.), Seagrass Research Methods, Chapter 8, UNESCO, Paris, pp. 55-60.

Perez, M. and J. Romero. 1992. Photosyntetic response to light and temperature of the seagrass *Cymodocea nodosa* and the prediction of its seasonality. Aquat. Bot. 43: 51-62.

Perez-Llorens, J.L. and F.X. Niell. 1993. Seasonal dynamics of biomass and nutrient content in the intertidal seagrass *Zostera noltii* Hornem. from Palmones River estuary, Spain. Aquat. Bot. 46: 49-66.

Perkins-Visser, E., T.G. Wolcott, and D.L. Wolcott. 1996. Nursery role of seagrass beds: enhanced growth of juvenile blue crabs (*Callinectes sapidus* Rathbun). J. Exp. Mar. Biol. Ecol. 198: 155-173.

Pihl, L. 1986. Exposure, vegetation and sediment as primary factors for mobile epibenthic faunal community structure and production in shallow marine soft bottom areas. Neth. J. Sea Res. 20, 75-83.

Pielou, E.C. 1966. The measurement of diversity in different types of biological collections. J. Theoret. Biol. 13, 131-144.

Pinckney, J.L. and F. Micheli. 1998. Microalgae on seagrass mimics: Does epiphyte community structure differ from live seagrass? J. Exp. Mar. Biol. Ecol. 221, 59-70.

Pollard, D.A. 1984. A review of ecological studies on seagrass-fish communities, with particular reference to recent studies in Australia. Aquat. Bot. 18: 3-42.

Robins, C.R., R.M. Bailey, C.E. Bond, J.R. Brooker, E.A. Lachner, R.N. Lea, and W.B. Scott. 1991. Common and scientific names of fishes rom the United States and Canada (5th ed). Amer. Fish. Soc. Spec. Publ. no. 20, 183 pp.

Rooker, J.R, S.A. Holt, M.A. Soto, and G.J. Holt. 1998. Postsettlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. Estuaries, 21:318-327.

Ross, S.T. 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia 2: 352-388.

Rozas, L.P. and T.J. Minello. 1998. Nekton use of salt marsh, seagrass, and nonvegetated habitats in a South Texas (USA) estuary. Bull. Mar. Sci. 63: 481-501.

SAS Institute. 1989. SAS language and procedures. SAS Institute, Inc., Cary, version 6.

SAS Institute. 1985. SAS user's guide: statistics. SAS Institute Inc., Cary, NC, version 5, 941 pp.

Schlotzhauer, S.D. and R.C. Littell. 1987. SAS System for elementary statistical analysis. SAS Institute Inc., Cary, NC, 416 pp.

Sheldrick, B.H. and C. Wang. 1993. Particle size distribution. In: M.R. Carter (Ed.) Soil sampling and methods of analysis. Ch. 47. Lewis Publishers, Boca Raton, pp. 499-511.

Sheridan, P.F. 1992. Comparative habitat utilization by estuarine macrofauna within the mangrove ecosystem of Rookery Bay, Florida. Bull. Mar. Sci. 50: 21-39.

Turner, S.J., J.E. Hewitt, M.R. Wilkinson, D.J. Morrisey, S.F. Thrush, V.J. Cummings, and G. Funnell. 1999. Seagrass patches and landscapes: the influence of wind-wave dynamics and hierarchical arrangements of spatial structure on macrofaunal seagrass communities. Estuaries 22: 1016-1032.

Vance, D.J., M.D.E. Haywood, D.S. Heales, R.A. Kenyon, and N.R. Loneragan. 1998. Seasonal and annual variation in abundance of postlarval and juvenile banana prawns *Penaeus merguiensis* and environmental variation in two estuaries in tropical northeastern Australia: a six year study. Mar. Ecol. Prog. Ser. 163: 21-36.

Vance, D.J., M.D.E. Haywood, D.S. Heales, and D.J. Staples. 1996. Seasonal and annual variation in abundance of postlarval and juvenile grooved tiger prawns *Penaeus semisulcatus* and environmental variation in the Embley River, Australia: a six year study. Mar. Ecol. Prog. Ser. 135: 43-55.

Vargas-Maldonado, I. and A.Yanez-Arancibia. 1987. Estructura de las comunidades de peces en sistemas de pastos marinos (*Thalassia testudinum*) de la Laguna de Terminos, Campeche, Mexico.An. Inst. Cienc. del Mar y Limnol. Univ. Nal. Autom. Mexico, 14: 181-196.

Weinstein, M.P. and K.L. Heck, Jr. 1979. Ichthyofauna of seagrass meadows along the Caribbean coast of Panama and in the Gulf of Mexico: composition, structure and community ecology. Mar. Biol. 50: 97-107.

Weinstein, M. P. and H.A. Brooks. 1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: community composition and structure. Mar. Ecol. Prog. Ser. 12: 15-27.

Williams, A.B., L.G. Abele, D.L. Felder Jr., H.H. Hobbs, R.B. Manning, P.A. McLaughlin, and I. Perez-Farfante. 1988. Common and scientific names of aquatic invertebrates from the United States and Canada: decapod crustaceans. Amer. Fish. Soc. Spec. Pub. no. 17, 77 pp.

Yanez-Arancibia, A., A.L. Lara-Dominguez, J.L. Rojas-Galaviz, P. Sanchez-Gil, J.W. Day Jr., and C.J. Madden. 1988. Seasonal biomass and diversity of estuarine fishes coupled with tropical habitat heterogeneity (southern Gulf of Mexico). J. Fish Biol. 33: 191-200.

Yanez-Arancibia, A., A.L. Lara-Dominguez, J.W. Day Jr. 1993. Interactions between mangrove and seagrass habitats mediated by estuarine nekton assemblages: coupling of primary and secondary production. Hydrobiologia, 264: 1-12.

Young, P.C. 1981. Temporal changes in the vagile epibenthic fauna of two seagrass meadows (*Zostera capricorni* and *Posidonia australis*). Mar. Ecol. Prog. Ser. 5: 91-102.

Zieman, J. C. and R.T. Zieman. 1989. The ecology of the seagrass meadows of the west coast of Florida: a community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85: 155 pp.

Zieman, J.C. 1975. Seasonal variation of turtle grass, *Thalassia testudinum* Koning, with reference to temperature and salinity effects. Aquat. Bot. 1: 107-123.

CHAPTER 5

SUMMARY

Seagrasses are extremely productive, diverse, and valuable marine resources. Among their distinguishing suite of characteristics they have an elevated primary and secondary productivity, a high abundance of organisms, and a high species diversity, all of which make them highly important for coastal human populations. Seagrass meadows are important for fishes and decapod crustaceans on the Atlantic coast of Guatemala as seagrasses provide them with increased food and refugia. In spite of all the benefits derived from seagrasses, coastal seagrass ecosystems are threatened by anthropogenic stressors.

The primary objectives of this study were (1) to quantify the nursery value of healthy seagrasses for fishes and macroinvertebrates in Bahia La Graciosa, on the Atlantic coast of Guatemala in a relatively pristine area, before further baseline degeneration, by comparing the biological diversity, community structure, and species abundances in sandy, shallow-water seagrass and adjacent bare-sand sites to test the null hypothesis of no faunal differences between habitat types; (2) to analyze the influences of differing degrees of exposure to wave action on the fish and decapod crustacean community structures, on the densities of common species, and on diel differences in species composition and abundance; and (3) to evaluate the influence of seagrass habitat types and seasonality (i.e., as reflected by rainy and dry periods) on the community structure of fishes and decapod crustaceans and to compare key environmental variables between seasons and habitat types

In Chapter 2, I described the diversity and abundance of fishes and macroinvertebrates inhabiting sandy, shallow water seagrass and adjacent bare-sand sites near the mouth of Bahia La Graciosa, and assessed the relative importance of turtle grass, *Thalassia testudinum*, meadows as nurseries. I also recorded microhabitat data, including mean depth, water temperature, turbidity, mid-water column velocity, distance to the shore, substrate percent sand content, salinity, dissolved oxygen concentration, and percent of the bottom covered by seagrass.

My results indicated that crustaceans and fishes were seven and 20 times more abundant, respectively, in seagrass compared to adjacent bare-sand sites. Only one of 19 fish species was found on bare-sand. Abundance, diversity, and evenness were significantly higher on seagrasses for both fishes and decapod crustaceans. Seagrass fishes included 19 species and were numerically dominated by juvenile Latin grunt, *Haemulon steindachneri*. The only fish present in bare-sand sites was shortchin stargazer, *Dactiloscopus poeyi*, which was second in overall abundance. The most abundant decapod crustacean species was the hermit crab, *Pagurus critinicornis*, followed by the longtail grass shrimp, *Periclimenes longicaudatus*, and the marsh grass shrimp, *Palemonetes vulgaris*.

The size of seagrass fishes indicated that the majority were early juveniles, supporting the hypothesis of seagrasses as an important nursery for fishes. Juvenile of organisms of local economic importance were commonly collected in the seagrass beds, including swimming crabs, penaeid shrimp, and fishes of the families Lutjanidae, Gerreidae, and Serranidae, which are of commercial importance and are captured for both

sale and consumption by local fishermen. This was the first quantitative study of seagrass fishes and macroinvertebrates conducted to assess the fishery value of seagrasses on Guatemala's Atlantic coast, an area of local economic and ecological importance currently under development. These results also documented the value of shallow-water seagrasses in terms of quality nursery areas for important commercial and forage species in Guatemala's Atlantic coast. This information would encourage resource managers and conservation agencies to guard seagrass meadows from the potential negative impacts of future coastal developments that can harm the health of these productive environments and the people that depend on them.

In Chapter 3, the utilization of seagrass meadows by fishes and decapod crustaceans was compared for exposed (beach) and protected (bay) estuarine habitat types near the mouth and inside of Bahia La Graciosa, Guatemala. The bay is characterized by extensive turtlegrass meadows over muddy substrates whereas around the bay mouth, a more exposed shoreline with sandy substrates also supports seagrass meadows.

Beach samples yielded 16 fish species, dominated by spotfin mojarra, *Eucinostomus argenteus*, banded blenny, *Paraclinus fasciatus*, shortchin stargazer, and emerald parrotfish, *Nicholsina usta*. Bay samples yielded twice as many fishes as beach samples and included 22 species dominated by spotfin mojarra, juvenile mojarra species, *Eucinostomus* spp., crested goby, *Lophogobius cyprinoides*, and hardhead silverside, *Atherinomorus stipes*. Total fish densities between beach and bay sites were similar; however, densities of four fishes between habitat types were significantly different. Beach samples also yielded 22 species of decapod crustaceans, dominated by southern pink

shrimp, *Farfantepenaeus notialis*, Dana swimming crab, *Callinectes danae*, night shrimp, *Ambidexter symmetricus*, and speck-claw decorator crab, *Microphrys bicornutus*. Bay samples yielded 19 species of crustaceans, and were dominated by banded snapping shrimp, *Alpheus armillatus*, southern pink shrimp, American grass shrimp, *Periclimenes americanus*, and knot-finger mud crab, *Panopeus lacustris*. Total crustaceans densities were similar between beach and bay sites; however, densities of five decapod crustacean species were significantly different between habitat types.

The structures of fish and decapod crustacean communities differed between exposed and protected habitat types. Bay samples resulted in more fish species, but beach samples had more decapod crustacean species, suggesting richer fish fauna in the bay and a richer crustacean fauna on the beach. Seven fishes were present only in beach samples, whereas thirteen were only found in bay samples. Decapod crustaceans in contrast, included three species found exclusively in the bay, but six species were only found in beach samples. Nevertheless, although decapod crustacean community diversity was significantly higher in beach samples, no significant differences were detected between beach and bay fish community diversities. Fish and decapod crustacean densities were related to eleven environmental variables in a factor analysis that explained 80% of the variance in five factors: a seagrass coverage axis, a substrate-distance-turbidity-depth axis, a temperature-dissolved oxygen axis, a current velocity axis, and a salinity axis. In multivariate analysis of complex environmental gradients, the ten most abundant fishes and crustaceans each used unique combinations of environmental variables.

No significant diel variations in community structure were detected when comparing sixteen night samples with day samples in an analysis of similarities of fish and decapod crustacean species. Nevertheless, analyses of variance for the ten most common fish and crustacean species indicated significant diel-by-habitat type interactions. No new decapod crustacean species were found uniquely in night samples, but three uncommon fish species were only collected at night, evidence of the importance of night sampling in studies of biodiversity of seagrass meadows.

The majority of the specimens collected in both habitat types in this study were juveniles, and many are of economic importance in the region, including spotfin mojarra, seabream, silver jenny, ground croaker, Dana swimming crab, southern white shrimp, and pink shrimp, supporting the hypothesis that seagrass meadows in protected environments in Bahia La Graciosa also serve a nursery function. Substantial differences in environmental variables between beach and bay helped to characterize these habitat types with exposure to wave action as the main variable responsible for the observed differences between habitat types. This in turn resulted in seagrass bed differences that affected fauna community structure. This is the first study of the effects of wave exposure on the rank order abundance patterns of tropical seagrass fishes and crustaceans.

Finally, in Chapter 4, I evaluated whether the habitat type effects already demonstrate were also observed across seasons. I evaluated the relative importances of habitat type and seasonality in seagrass fish and decapod crustacean community structures. Protected (bay) and exposed (beach) habitat types were sampled during rainy and dry seasons in and around Bahia La Graciosa. Seasonality in the study area is characterized by

rainy (June - November) and dry (December - May) months, although rain occurs throughout the year. My results indicated that environmental conditions differed significantly inside and outside the bay and seasonally. Faunal collections resulted in a total of 74 species, including 44 fish and 30 crustacean species. The ten most abundant nekton species accounted for 62% of all individuals and included (in order of abundance) banded snapping shrimp, spotfin mojarra, crested goby, southern pink shrimp, juvenile mojarra species, Dana swimming crab, hardhead silverside, knot-finger mud crab, banded blenny, *Paraclinus fasciatus*, and goldline blenny, *Malacoctenus aurolineatus*. Over half of the species (55%) were present in both seasons and almost half of the species (46%) were present in both habitat types. The fish community structure in the study area was significantly affected by both habitat type characteristics and seasonal variation but decapod crustacean community structure was only affected by habitat characteristics. In general, the influence of habitat type appeared to have a stronger effect than season, particularly on crustaceans, in determining community structure.

Significant interactions were detected between season and habitat type effects for the density of the ten most common fishes, and the ten most common decapod crustaceans, together with total fishes and total crustaceans. Moreover, significant differences between the densities of habitat type and season combinations were detected for several individual species. Differences in faunal composition between seasons and habitat types were basically expressed in terms of species composition, as total fish or total crustacean densities differed little. Regarding individual species densities, the most common fish, spotfin mojarra, was the only species that showed a significant main effect

for season, and the second most abundant fish, crested goby, was the only species that showed a significant main effect for habitat type.

Fish and decapod crustacean densities were related to eleven environmental variables in a factor analysis that explained 71% of the environmental variance in four factors: a seagrass coverage axis, a habitat type axis, and two seasonality axes. In this study on the Atlantic coast of Guatemala, where the dry season was poorly demarcated, seasonality was not as important as habitat type in structuring the communities of seagrass fishes and decapod crustaceans. This study is among the first documenting the significance of changes in tropical seagrass community structures related to habitat type and seasonality.

In conclusion, these studies documented the value of shallow-water seagrasses in terms of quality nursery areas for important commercial and forage species in Guatemala's Atlantic coast. Substantial environmental differences between beach and bay habitat types, related to exposure to wave action, were important in structuring seagrass meadows which in turn resulted in changes in fauna community structure. Finally, seasonality was found to be secondary to habitat type in structuring the communities of seagrass fishes and decapod crustaceans in this study on the Atlantic coast of Guatemala. The value of shallow water seagrasses shown here may be extended to nearby deeper water seagrasses, as previous studies using less quantitatively sampling methods have shown in other areas. Nevertheless, the expansion of this study's finding to deeper water seagrass habitats will have to rely on the permanence of suitable water quality conditions.

APPENDIX

LETTER OF PERMISSION

21 March 2000

Alejandro Arrivillaga
Department of Oceanography and Coastal Sciences
Louisiana State University
Baton Rouge, LA 70803

RE: Arrivillaga, A. and D. M. Baltz. 1999. Comparison of fishes and macroinvertebrates on seagrass and bare-sand sites on Guatemala's Atlantic coast. Bulletin of Marine Science 65(2): 301-319.

Dear Mr. Arrivilaga:

This letter gives you permission to include the referenced article in your dissertation. It will require a full citation and acknowlegment of publication in the Bulletin of Marine Science. This permission is limited to your dissertation only. Any other use of the article will require a separate request for permission.

Very sincerely,

Samuel C. Snedaker

Prof. Samuel C. Snedaker, Editor

cc: Copyright file

Rosenstiel School of Marine and Atmospheric Science
Bulletin of Marine Science
4600 Rickenbacker Causeway
Miami, Florida 33149-1098 USA
Phone: 305-361-4624 • Fax: 305-361-4600 • E-mail: bms@rsmas.miami.edu

VITA

Alejandro Arrivillaga was born on August 23, 1960, in Guatemala City, Guatemala. During his high school years a very enlightening biology teacher, together with the books and videos of the late Capitan Jacques Custeau developed his fascination with marine life. In 1978 he enrolled in the aquaculture program at the Universidad de San Carlos de Guatemala and experienced for three years life in a fishing village on the Pacific coast of Guatemala. That experience sealed his eternal bond with aquatic sciences. He graduated in 1980 with a University Technical Degree in Aquaculture. Latter on, in 1985, he obtained his bachelor's degree in science from the Universidad Del Valle de Guatemala in Guatemala City. He then obtained his master's degree in 1987, from the Centro de Investigacion y Estudios Avanzados, CINVESTAV, in Merida, Yucatan, Mexico, where he worked on fish culture and nutrition. Then he returned to his home country, where he earned a Professorship in the Biology Department of the San Carlos University. He worked there from 1988 until 1992, when he was awarded a Fulbright-LASPAU scholarship. He enrolled in the graduate school at Louisiana State University, majoring in oceanography and coastal sciences, and minoring in experimental statistics and fisheries. He currently is currently conducting an Academic Training Program, working at the post doctorate level at the National Wetlands Research Center in Lafayette, Louisiana. He is married to Catalina Lopez and has two sons, Javier and Adrian. In May, 2000, he will receive the degree of Doctor of Philosophy.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Alejandro Arrivillaga

Major Field: Oceanography and Coastal Sciences

Title of Dissertation: Ecology of Seagrass Fishes and Macroinvertebrates on Guatemala's Atlantic Coast

Approved:

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

March 16, 2000